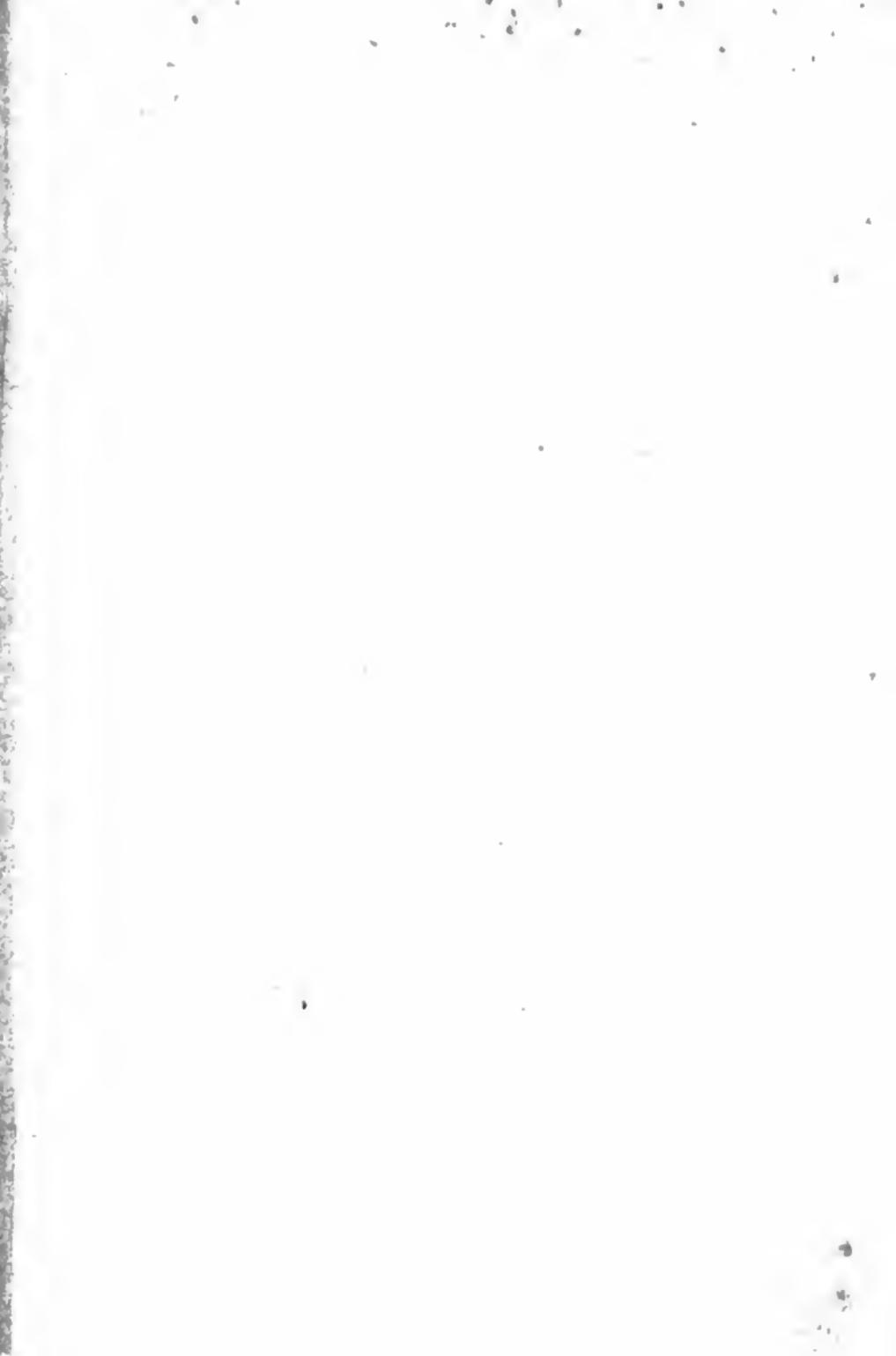


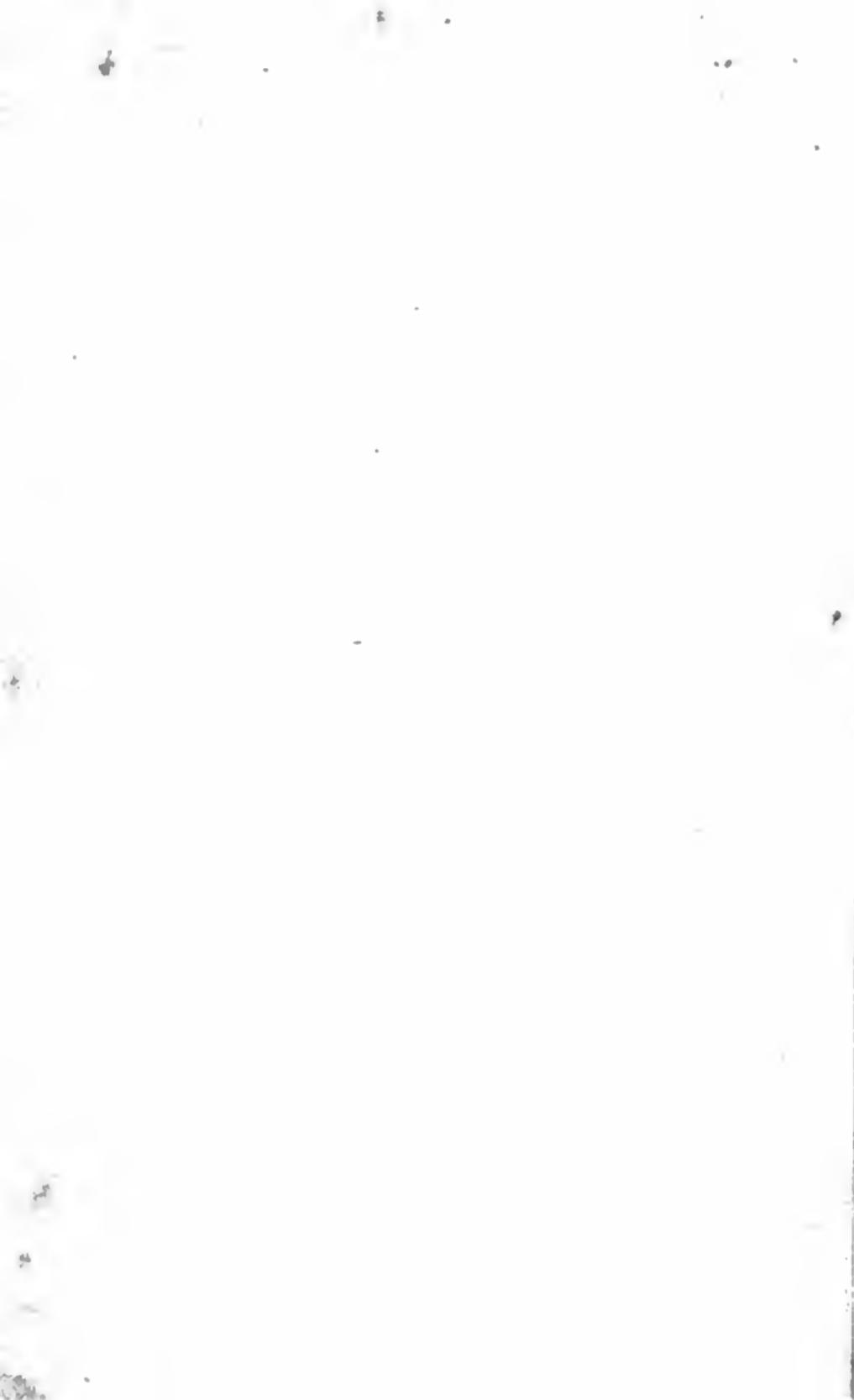
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EVOLUTION AND CHRISTIANS

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HISTORICAL ASPECTS OF ORGANIC EVOLUTION, 1952

LIFE AND ITS ORIGIN, 1958

EVOLUTION AND CHRISTIANS

PHILIP G. FOTHERGILL, F.R.S.E.
Department of Botany, King's College, Newcastle-upon-Tyne

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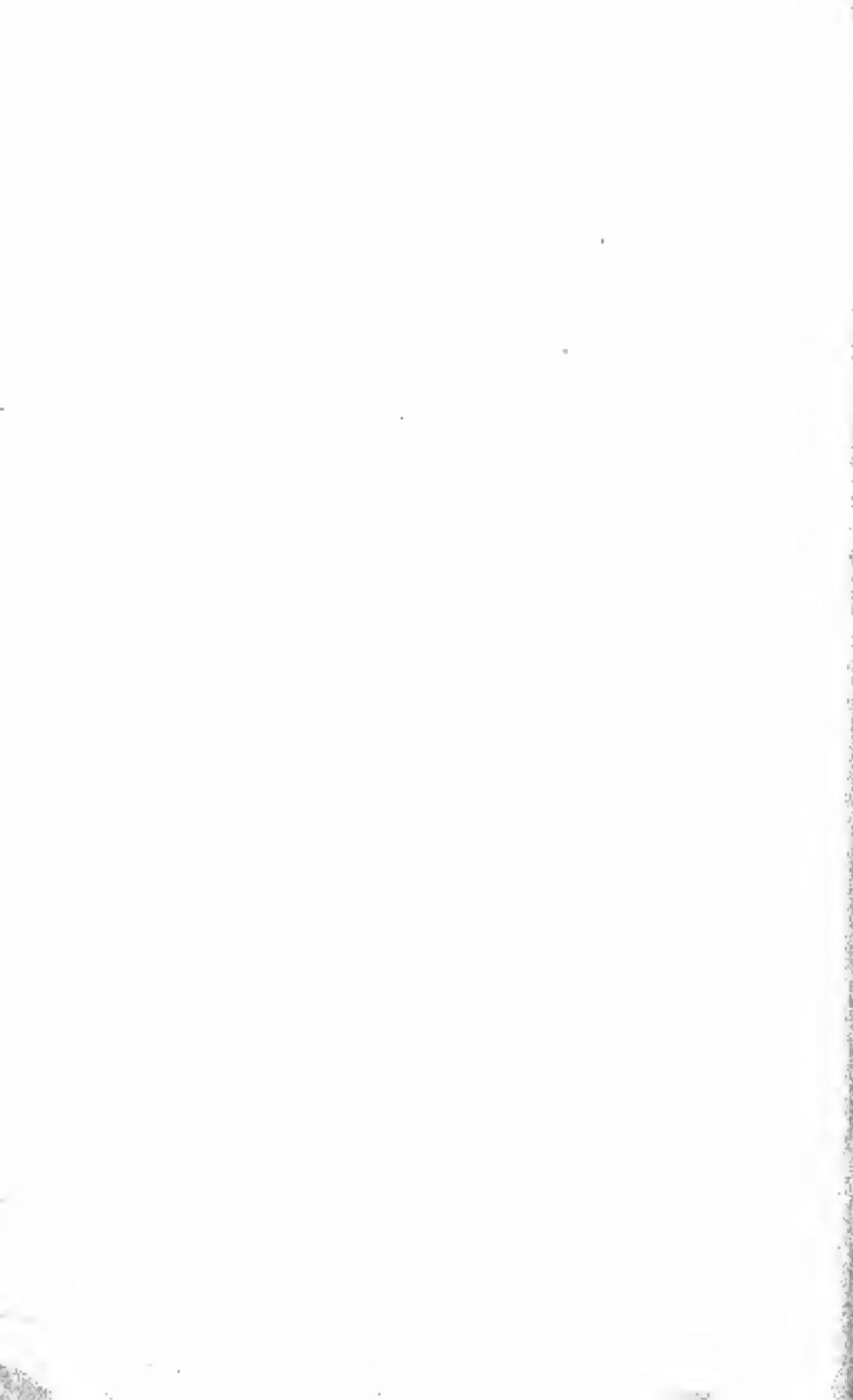
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Omnia per ipsum facta sunt: et sine
ipso factum est nihil, quod factum est.

TO MY WIFE
AND THE 'GANG'



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INTRODUCTION

THIS book is written for Christians who are interested in the biological theory of evolution and its implications. I have written as a Roman Catholic and hence my information regarding the theological and philosophical parts of the book has been mostly obtained from Catholic sources. But inasmuch as the interpretation of evolution may affect the Christian and not specifically denominational outlook, a Catholic approach to the subject should be of interest to all Christians particularly regarding the origin of man which has received detailed treatment. I have not attempted to cover the whole field in this respect.

Parts of the book are not easy to read, and it is not meant to be a 'popular' book on the subject. It should be useful to scientifically-minded and intelligent laymen and also to many students. Sixth-form students taking biological subjects should find many parts of the book informative, providing much material for debates or discussions. Many Church and scholastic groups should also find it useful in this respect but, although both laymen and sixth formers may find some parts of the book rather advanced, these parts could be omitted without detriment to many of the other topics discussed. To biologists and University students the book gives a point of view which has been neglected in the past, and it should increase their realization of the potentialities of the subject of evolution. Not all biologists, however, are necessarily evolutionary specialists but all should find the philosophical and theological parts interesting. Biology and evolution nowadays are highly complicated subjects and it is useless to expect to learn anything really worthwhile about them without a good deal of mental effort. The main reasons for this difficulty are that evolution is now very technical and it is such a vast conception embracing several branches of science, and its implications spread into non-scientific domains. One of my chief aims is to present in a single volume of manageable size enough information about evolution and its implications for man, parts of which will be useful to one type of reader and parts to another type, while many readers will be able to appreciate the whole book. The book thus

INTRODUCTION

brings together important information about evolution and its relation to parts of philosophy and theology which is generally available only in separate and diverse volumes. Hence in a book of this kind a writer must of necessity choose his material from among an abundance of information, and his choice, in part at least, must be subjective. Some readers may thus find that some point which they consider to be important has been omitted. I hope that critics and reviewers will bear this difficulty in mind. To overcome it the book would have to be greatly enlarged, thus defeating one of its aims.

I only claim to be writing as a Catholic professional biologist who has spent a good deal of his life in a quasi-philosophical atmosphere, and hence I ask the professional philosopher's toleration if there is anything in the book to make him smile. I have ventured into the philosophical field before and realize the demands the philosopher makes on the use of language. I ask for the same toleration, but with even greater force, for the theological parts of the book, and on matters touching Faith I claim no originality. I submit willingly to the authority of my superiors in such matters. The book is not written specifically for Catholic philosophers and theologians, but they should be able to obtain sound information from the biological parts of the book which may be useful to them. The opinions of a Catholic biologist about the status and implications of evolutionary theory should also be of interest to them.

I think it is appropriate in a book of this kind, published in the centenary period of the publication of Charles Darwin's *Origin of Species*, to include in it a serious, but fairly short, version of the kind of evidence on which the theory of evolution is based. There is a tendency nowadays for some writers on evolution to omit the 'evidence' with the excuse that there are many textbooks containing it, or that the theory is so obvious and widely accepted that it is no longer necessary to give the evidence for it. It is, however, really surprising how few available textbooks there are giving concise and accurate accounts of the evolutionary evidence and including at least some of the modern extensions, but which are yet long enough to impart some real information. It may be surprising to many evolutionists to be told that there are in fact quite a number of intelligent people who do not consider that evolution is anything more than a working hypothesis. Even

INTRODUCTION

when the evidence is given in textbooks, criticisms and difficulties are often omitted, except in the older Darwinian literature where emphasis was so often laid on evolution versus special creationism. In this literature the difficulty raised by the critic was so often left in the air.

I have, therefore, tried to introduce some criticisms and difficulties into my account of the evidence—very many more could be given. I do not expect all biologists to agree with all my opinions, but I hope thereby that my colleagues do not get the impression that I am a sceptic, which I am not, although I do not by any means accept everything that is written about evolution. This remark applies with greater force when an evolutionary writer leaves the purely biological field. In evolutionary matters there is much room for opinion and I have not hesitated to give my own which may not necessarily coincide with the more popular biological opinion. I think it is clear from the text when I am stating a personal opinion.

I would like my book to be at least one biologist's acknowledgement of the great work of Charles Darwin who did a tremendous service to biology. Darwin was a genius, and like all such people he was misunderstood by many others, and like all geniuses he had to suffer the adverse effects of criticism, but he gave a theory to biology which the writer thinks will ultimately prove to be fruitful and bring religion and biology, especially in the sense of the study of man, together in a harmony beneficial to both and to the lasting advantage of both, because truth is indivisible.



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King's College,
Newcastle-upon-Tyne,
October 1959.
A.M.D.G.

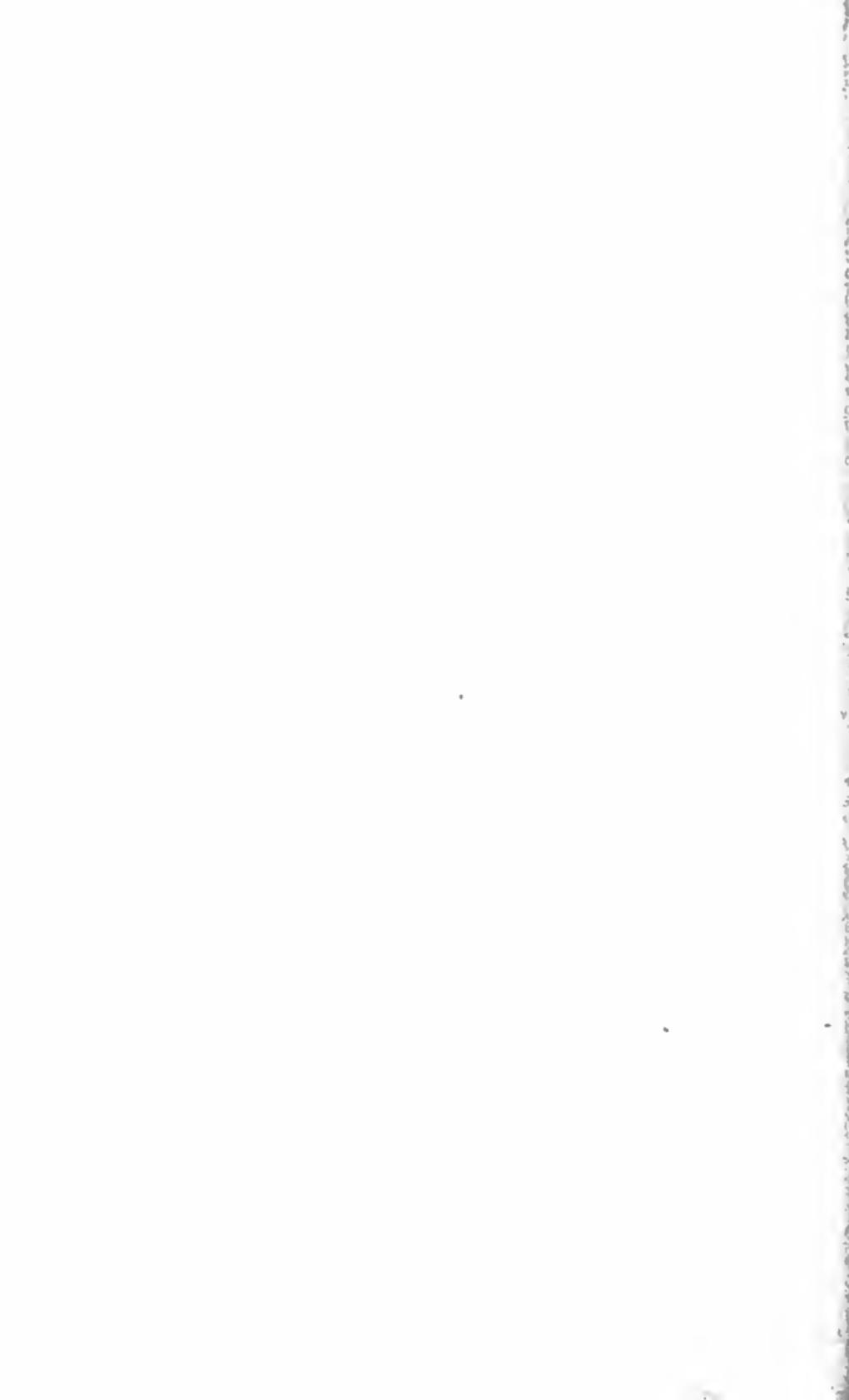
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EVOLUTION

A gas, a flash—
Nature's primeval mass;
By fat crawled forth
A quivering mass of gel.
Through the years from this arose
Fish, frog and feather,
And last of all came Man,
With strength, beauty, brain,
To dominate and explain
The vibrant plasm.
At God's command all nature's array
Holds sway
In ordered fashion.
But genius, wisdom, calculation
Through the ages engendered
An idea of lawful change
In Darwin and Wallace
Of selectio-mutation,
'Omnis vivum ex vivo,'
Being, becoming being,
In a word—evolution!

(Margaret M. Fothergill, VIA,
La Sagesse Convent High School,
Newcastle-upon-Tyne)



Chapter I

Scientific Method, Religion and Biology

1. INTRODUCTION

IN A foreword to a collective work on evolution Henry Fairfield Osborn, who was a pupil of T. H. Huxley, and who became one of the greatest of American biologists, said of the word *evolution*: 'No word in any language at the present time is so comprehensive as this; few words are so misunderstood.'¹ Statements of this type are rarely literally true, but nevertheless they serve their purpose, and Osborn succeeds in making us stop to think. We tend to ask ourselves: what does he mean by this statement? And so our interest is aroused. Osborn's last phrase is true and indeed for many partially informed people the word *evolution* conjures up thoughts of the discrediting of religion, because they seem anxious to seek a way of escape from the responsibilities implied in Christian teachings. On the other hand, some religious people, equally misinformed, look with disdain on those who hold evolutionary views; they consider them to be supporters of a pernicious, atheistic doctrine and enemies of Christianity. Yet it is a fact that evolutionary theory is one of the great generalizations of biology, i.e. of the science that deals with all living things, including man. This is the centenary period of the publication by Charles Darwin of his great book *The Origin of Species*. This book was sold out on the very first day of publication, and subsequently it went through numerous editions right up to the present time—a new issue was published by Everyman's Library in 1956. From 1859 onwards a new outlook seized hold of biologists; the rate of biological research increased very rapidly,

¹ 1929. Full reference to books and papers mentioned in the text will be found in the bibliography. To find any particular reference refer to the date in the footnote at the bottom of the appropriate page in the text, or given in brackets after a name in the text, then look in the bibliography under the name concerned with the year corresponding to the footnote. As far as possible only standard abbreviations are used for all periodicals. These abbreviations will be found in the *World List of Scientific Periodicals*, 3rd ed. by W. A. Smith, F. L. Kent and G. B. Stratton, publ. Butterworth Scientific Publications, London, 1952.

and biology began to take its place along with chemistry and physics as a science in its own right. The genius of Darwin lay in the stimulation which his main ideas gave to biology and he was not essentially an irreligious man. He was not personally antagonistic to religion. Thus there must be a reason, or reasons, why even the mention of evolution can sometimes produce strong emotional reactions among diverse people.

It is one of the objects of this book to attempt to give a reasoned modern account of evolutionary theory in which its relation to, or its bearing on, the Christian religion will be stated and examined. What we wish to obtain is a balanced outlook on the matter, because we are convinced that both religion and evolution are true and valid spheres of knowledge. We also are convinced that our scientific ideas should lead us to God and not away from Him. But first the views we have already put forward require an explanation.

Let us then first of all look briefly at the broader issues of our subject, that is, at the general relation of religion to science. Christianity implies fullness of union with Christ, which means that by faith and reason we believe in the truths that Christ taught, and we attempt to model our lives on His teachings and on His example. As Catholics we believe that union with the Catholic Church enables us to do this most efficiently because the Church was instituted by Christ to guide us along the right path and to prevent us from falling into error. We are members of the Mystical Body of Christ and hence we have the means and the certainty of salvation provided we do not sever ourselves from that Body. Now what is science? Simply expressed and in the historical sense, science is one way of trying to fathom the nature of the world, and indeed of the universe, and of the material things in it. The scientist wants to give an explanation of the world and its contents. He wishes to do this, firstly, to increase our knowledge; secondly, to better the material conditions under which men live by mastery of the elements of those conditions; and thirdly, for delight, pleasure or the earning of one's livelihood. The scientist is not a member of any Universal Society, but he feels himself to be so.

In these senses both religion and science are partly theoretical and partly practical. But there is this important difference: the Christian religion is authoritative and is based on Revelation,

SCIENTIFIC METHOD, RELIGION AND BIOLOGY

Reason and Tradition which springs ultimately from its Founder. The Christian religion gives a sufficient explanation of man's nature in terms of his ultimate end which is to see God. On the other hand, science has no means of determining man's ultimate end, and without Revelation it cannot obtain a complete picture of the nature of man. Science is primarily concerned with things and with phenomena in nature. Thus science is based on reason and scientists proceed by using what are called the inductive and the hypothetico-deductive methods. To understand what science is and how it works and the value of its conclusions it is necessary to know what is meant exactly by these scientific methods. Hence a short account of them is now given.

2. THE INDUCTIVE AND HYPOTHETICO-DEDUCTIVE METHODS OF SCIENCE

The scientific methods seek to obtain truth with regard to nature through definite steps involving *observation* (experience), *measurement* (experiment) and *inference* leading to an hypothesis. For example, we may make a sufficient number of observations that tall Scandinavians will have both long legs and long arms. That is, in this inductive method we have reasoned from a particular (or from a few particulars) to a general case. If we have made, or make, a large number of observations on Scandinavian and other peoples too we may then form a hypothesis and say that all tall men will have long legs and arms. This hypothesis could now be extended to include the relation of tall men to long appendages or joints, and we may be tempted to use it as the starting point for other observations about long fingers and long joints, and if it held we could finally conclude that all tall men have long appendages. If we found a human fossil comprising a few long leg and finger bones we could assert that the man who had possessed them had been tall, which conclusion would help the anatomist to reconstruct the individual.

The relation of the inductive method to science just illustrated, however, proves to be too simple and philosophes vary in their opinions about this relationship. Some even take an extreme view; for example, J. O. Wisdom¹ said that 'induction plays no part in science'. He will allow that there may be a pattern of

inductive inference but no method of induction in science. One of the main reasons why he discarded induction was because he found that observations were not generally made unless the observer saw in them some conflict with attitudes or expectations already held, i.e. the observer already had a hypothesis before he made his observations and these were made to test the hypothesis. The path followed was still from particulars to a general and so there may be a pattern of inductive inference, but the process began with a generalization. As Wisdom¹ wrote:

The hypothesis is expressed in a general statement, some relevant observations are made and expressed in a particular statement, and a conclusion, which is sometimes a prediction, is *deduced* and finally tested by experience. The requirements of the system are then, (a) a general expectation, (b) an observation, and (c) a valid deduction.

The conclusion then becomes the fact to be 'explained' and the hypothesis is the 'scientific explanation' of it. From this it follows that if a description of a fact can be put as the conclusion of a valid deductive inference then the fact can be made the premiss of the inference and the statement becomes the scientific explanation of the fact. This method of reasoning is called the hypothetico-deductive method.

G. von Wright,² however, has pointed out that the extreme views of Wisdom may not be valid. He showed that generalizations arise from two types of situations involving (a) a simple inductive method proceeding from particular to general, and (b) a hypothetical method which cannot proceed until it introduces a new concept or hypothesis. The situation becomes resolved if the results verify the hypothesis. This is a method of hypothesis plus deduction. But the hypothesis concerned in the method has also a conjectural aspect which should make predictions possible. As Wright³ wrote:

Thus hypothesis in science frequently has a double function. It introduces a new idea to account for observed data. And it makes *conjectures* about the unobserved. The first function presupposes that an invention or discovery has been made. And inventions are, as Whewell said, 'happy guesses', or 'leaps which are out of the reach of method'. To fulfil the second function, is to reason inductively.

Hence induction is seen to be present in the hypothetico-deductive method itself.

¹ 1952, p. 51.

² 1957.

³ 1957, p. 306.

SCIENTIFIC METHOD, RELIGION AND BIOLOGY

The writer, who can give only a personal opinion, considers that biology in general, and evolution in particular, use both these methods in an interwoven scheme which as it becomes perfected tends to enlist the aid of mathematics which is deductive. In practice in biology methods generally used obviously involve many comparisons between like things and in doing this we are examining a sample from among many possibles. Thus analogy is used and the things compared may belong to different classes and so analogy may be misused or pressed too far, as Agnes Arber¹ pointed out. According to her there are many examples of over-emphasis of analogies in biology. The mistake seems to lie in making the analogy an identity; the inference drawn from the analogy must then be partially false. For example, we may examine many samples of backboned animals and learn that their skeletons are very like in many respects; a legitimate inference would be that such animals are built around a common plan. But the analogy of likeness of the skeletons is often taken to indicate an identity and a conclusion is then advanced that the likeness is due to a common ancestry or inheritance. This conclusion may be true, but it does not follow of necessity from the likenesses of the bones. Many biologists in previous times knew of the likenesses but never proceeded beyond the common plan inference, and a modern biologist, W. R. Thompson,² also sees no compelling reason to agree that likeness spells genetic affinity.

Such a conclusion about common ancestry can be made only when other concepts are introduced into the argument. It seems that a system of induction combined with hypothetico-deductive arguments is very complex and it is easy to see that in practice such arguments tend to become overburdened and circular, and in fact may often beg the question. For example, a basic assumption of Darwinian and Neo-Darwinian theory assumes a likeness, nay, even an identity, between 'artificial' human selection which changes things and 'natural' selection which is also believed to change things. Having inferred the identity and attempted to test it (in practice this is done by eliminating opposition) then much of evolutionary theory is built up, and there is now such a mass of detail which has accumulated over a long period of time that the original over-emphasis on an analogy has been lost sight of. In a sense then much of evolutionary theory begs the question by

¹ 1914. ² 1936.

assuming evolution before it has been proved. The hypothesis is present at the beginning of the argument as it should be in hypothetico-deductive method, and no doubt this method is common in science, but there do seem to be logical dangers in its use unless strict safeguards are taken.

If a hypothesis is used frequently and successfully in science it becomes established and is then regarded as a theory. A well-established theory which stands the test of time is often regarded as a 'law' of nature. But some people consider that it is not correct to use this word in this sense—a law is something given and has compulsive force. Perhaps a better word would be 'rule'. The essential feature of such a rule is that it should work and be of practical use to scientists in their investigations on similar or related observations to those which led to the formulation of the rule, and which will enable them to make important predictions. A theory is itself a possible interpretation of the facts of observation, but as Caldin¹ pointed out, interpretations, inasmuch as they are further generalizations from the data, often go beyond the actual evidence presented. As they are proceeding from a particular to a general they are reaching out into the unknown but still in an empirical fashion. On the other hand, further interpretation may be given to a theory so as greatly to extend its meaning and this may be done by scientists or by philosophers to lead to a further and more universal generalization. For example, some geneticists, because they find that many characteristics and functions of organisms are deterministic, controlled by genes, consider also that all human actions are determined, not by the individual, but by his genetic make-up.² Again, the theory of evolution is a wide generalization which in a sense unites the whole of living things, including man, into one grandiose scheme. Such a theory in this wide sense is itself an interpretation of the whole of organic nature, or at least has within itself the interpretation of organic nature at the phenomenological level. But there are other levels at which an interpretation of nature could be made especially if the nature of man were included, and these levels would have to be considered before a comprehensive meaning could be given to evolution. By this time, however, the scientific method would have been left behind and philosophical methods would have to be used if progress were to be made. This

¹ 1949.

² See Darlington, 1953.

last observation gives us an indication of the limitations of science. Thus a theory or interpretation in science does not then necessarily give the final answer, and this point also follows from the fact that scientists do not assent to absolute truth in science: their truth is always relative. Hence although science seeks after truth, and although it may find it, it does not give *certainty*—it gives only a *degree of certitude*, which, according to the evidence, may be more certain or less certain. Any scientific theory and its wider applications, as history shows, may be scrapped as knowledge of nature widens. This does not mean that a discarded theory did not have value in its day, as the old Ptolemaic astronomical theory shows—it was quite useful in its day. Incidentally, we may note how old ideas persist in common language for we still talk of the sun rising and setting when of course the sun does not move. We may quote Agnes Arber¹ in this regard who wrote:

The acceptance of an hypothesis, and its resulting adoption as a theory, do not mean that it is 'proved', and it is at least a possible view that it is to 'authenticate', or to 'justify', rather than to 'prove', which should be the biologist's aim. . . . In the purely biological, and thus autonomous, aspects of science, we are, strictly speaking, outside the pale of logic, and there can be no question of certainty or proof. We cannot even reach probabilities expressible in mathematical terms; we can only look for psychological probability.

The true scientist would be the first to acknowledge this limitation of his science.

We can approach the question of the limitations of science from another point of view. In general the capability for making predictions would indicate a high degree of certitude for the theory on which the predictions were based. But it should be clear that, if a prediction is *possible*, then it presupposes, or presumes, a certain orderliness in nature—one cannot have a law based on chaos. When a scientist decides to carry out some research work on some problem, he first of all reads around the subject concerned, then he plans his experiments and carries them out on the basis of expectancy. He expects to get results of a certain kind, and he is prepared for them. Throughout all these elaborate preparations the scientist knows that certain things will happen or will not happen, otherwise he could not make any

¹ 1954, p. 32.

plans at all. He knows there is a certain orderly behaviour in the things he is dealing with. Normally he realizes, as we all do, that there is order in nature from his own common-sense. While his actual experiments may give an illustration of order in nature, he can never, by the method of experiment, *prove* it, for the simple reason that the scientific method itself is only possible because of order in nature—the lesser cannot demonstrate the greater. Without order induction and hypothetico-deduction would be impossible. Actually philosophers have long used their methods to show that there is order. It seems that it can really only be formally established through metaphysics.¹ Hence in the final analysis science is limited by its own methods and laws, and the justification for these rests ultimately on philosophy, not on science. The roots of science are metaphysical, not empirical and observational.

It is very important to understand the truth of these observations about the scientific methods and to understand them thoroughly. A lack of appreciation of the limits of science in their fundamental aspects has undoubtedly led to much pseudo-science and confusion in some scientific writings, especially those on such a topic as evolution. It is just as important, however, to realize also that, while the bases of science may be philosophical, science is not metaphysics and metaphysics may only treat with science incidentally. Such a situation at first sight would seem to be paradoxical. What the situation really indicates is the necessity for another branch of knowledge which abstracts from science and connects to philosophy. That is, there is a necessity for a philosophy of nature.

The need for such a philosophy has really been recognized from early times. In the early days of philosophy even science itself was absorbed into philosophy generally, with the result that science became subject to philosophy, lost its identity and suffered much harm. In later days, with the rise of science, the philosophy of nature became absorbed into science and lost its identity, but, as science became so successful in a practical sense, philosophy suffered great harm and has even been denied recognition. Nowadays the philosophy of nature is coming to the fore again as a branch of knowledge distinct from other branches of philosophy.

These and similar important points are discussed in detail by

¹ Caildin, 1949.

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Maritain,¹ but in order to clarify the argument we can do no better than to quote him in a particularly informative passage. He wrote:

The sciences of phenomena thus bear witness to the fact that nature is knowable and that they only know it in an essentially unsatisfying way. In this measure, therefore, they require to be completed by another knowledge of the same sensible universe, which will be an ontological knowledge—in truth, a philosophy of nature. Not only do we say that the sciences deepen and quicken the desire of the intelligence to pass to deeper and higher truths, just as the philosophy of nature itself quickens the desire of the intelligence to pass to metaphysics, but we say also that inasmuch as they are knowledge ordered to a certain term, the experimental sciences require to be completed, not of course so far as concerns their own proper rule of explanation, or the formal object which *specifies* them, but in regard to the term in which they issue, which is the sensible and the real. In so far as it is mutable and corruptible, the latter is known in an essentially unsatisfying way with the help of the vocabulary which is proper to empirical knowledge. Thus, this knowledge must be completed by another which exists at the first degree of intellectual abstraction and will grasp the intelligibility of the real which is thus proposed to it.

And, of course, the inverse is just as true because the philosophy of nature cannot stand by itself, it must be completed by the natural sciences. The explanations we have given here to show the limitations of science have probably been much too simplified, but they have been given primarily to emphasize again the fallacy behind any proposition which seeks to show that science by itself is self-sufficient and gives a complete explanation of all things. This is essentially the position taken up by materialists or neo-positivists, scientific humanists and those biologists and other scientists who seek to find in science a *source* for religious ideas. It must be noted, however, that it is not implied that a scientist may not deal with his observations, measurements and so on, on a purely objective level without reference to nature in general. He is perfectly justified in doing so and in fact he ordinarily does so; the scientist then may not be concerned with any philosophy of nature, but in so far as he is not concerned the less do his generalizations bear any relation to reality in any but the strictly scientific field.

¹ 1934, pp. 52-53.

On the other hand, the Christian Religion is given by Revelation and Faith, which is our acceptance of Revelation. Further, an established basic feature of man is that he comprises a physical body subject to laws governing such bodies and a spiritual, intellectual soul which is immaterial. As we are writing for Christians there is no need to develop arguments for the existence of the soul. Religion seeks the truth about God and the connection of man's soul to his body and to God in relation to his last end. As the soul is immaterial, science which deals only with material things can say nothing about it, although it may, of course, consider some of the effects which it has on the physical body. As regards religion and the complete human being, science is important only in so far as scientific conclusions lead to a consideration of (a) the nature of man in the biological and psychological senses which may have a bearing on the intellectual soul and its free will, and (b) primitive religions which may be the biological expression of primitive peoples grasping for Faith. Revealed Religion and the Incarnation are indeed facts which can never be under scientific experimentation.

3. CONFLICT BETWEEN SCIENCE AND RELIGION

Both religion and science are concerned with truth and with the practical consequences following directly from those truths. Hence, as truths cannot be mutually contradictory, they cannot be antagonistic, even though science is concerned rather with relative truth and revealed religion attains to absolute truth. But these facts do not mean that there cannot be an apparent antagonism between religion and science, for obviously there has been for many years. Scientists and philosophers of religion recognize that there is conflict between them which leads to a fundamental problem. This problem is concerned with the status, method and content of the philosophy of nature. We have already mentioned this problem, but we should say further that without a philosophy of nature the conflict is a real one, but with such a philosophy it becomes an apparent one, and is finally resolved. To give a full explanation of the conflict in these terms would involve us in discussions in the philosophy of nature which are beyond the short accounts given here. It is the conflict which we wish to mention specifically. The explanation of it is complex, but

yet basically there are many features of the apparent conflict between science and religion which can be dealt with at a much simpler level and we will try to explain some of these features.

Bearing in mind again that a complete solution to the conflict between religion and science may be found in the philosophy of nature we may still say that for ordinary purposes and at a lower level much of the conflict and many of the apparent contradictions are superficial and are often due to misunderstanding either by scientists, or by religious people, or both. Further, in the scientific and non-scientific worlds, there are anti-religious people who use scientific knowledge to attack religion whenever they think the opportunity has arisen. If a conflict between some scientific finding and religion is encountered through some means, it is always a good policy to enquire into the antecedents of the advocate, and then to examine critically the contents of his argument. As a rule exaggeration, misrepresentation of the facts, over-emphasis, or even ignorance of religious teachings, will be found to be the real point at issue. Thus in many cases the seeming conflict will disappear, or at most remain doubtful. In the latter case a conclusion should be postponed until the matter is reasonably beyond dispute. T. Sherlock¹ traced such misunderstandings back to the Middle Ages. In those times the scholastic philosophers, translating the philosophy of Aristotle into Latin from the Arabic, incorporated much of his thought into their own philosophic system. At the same time, however, they also adopted Aristotle's 'physics', which as time went on was shown to be in the main wrong. But the medieval scholastic felt obliged to oppose the new physical views merely because these views represented, as he thought, an attack on the whole successful Aristotelian system, and hence, a habit of opposition arose. Another reason for the apparent conflict of religion and science lies in the fact that religious thinkers have learnt to be wary of new scientific theories for many of these theories are not permanent, and it would be foolish to argue about fundamental beliefs in the light of some impermanent theory. It is for this reason that the Catholic Church often seems slow to take up some new scientific finding—time is a great tester and in any case no scientific finding could possibly affect any basic doctrine—it might perhaps affect the interpretation of a doctrine but never the

¹ 1940, p. 6.

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reality of it. Hence, in many ways the so-called antagonism between religion and science is often a conflict of minds and rarely a real conflict of facts.

It is of the utmost importance to distinguish between fact and theory in science, but often this is not easy. The scientist observes things, he makes measurements, and thus he collects many facts, indisputable facts. For example, he may cut a thin section of a piece of a plant stem and, using his microscope, he may examine the cells, describe them and put them into their various types. Or, he can measure the amount of heat it requires to raise the temperature of a given body through one degree and repeat this measurement under various conditions. And so on. Facts like these which the scientist collects may be very interesting to him, but they are not of much value by themselves. They assume a value when united together with other facts. Bare facts are like a heap of bricks lying on the ground. We see their use when they are put together to form a house. Often when the scientific facts are put together their value becomes obvious by enabling the scientist to construct a *theory*. A theory, as already pointed out, is a generalization which enables the scientist to obtain new and possibly more important facts. A scientific theory is 'fact' in the same sense as the basic facts on which it is based are facts. The basic facts are founded on observation, but the theory is primarily a mental construction, and a good theory, that is, one founded on a great many facts, gives the scientist a greater insight into the workings of nature. It gives him an explanation of some natural phenomenon and he then begins to understand the problem he is dealing with.

Thus a theory is a working proposition which the scientist accepts for the time being to enable him to progress further in his work. It is the key to his progress, but it is at all times liable to modification or rejection as new facts emerge. All scientists know this, of course, but many laymen do not seem to realize it. To say that some religious truth is wrong because of some scientific theory is illogical. The theory of evolution, for example, could never disprove any fundamental religious dogma. Finally, extreme prejudice sometimes contributes to this conflict of science and religion. Strong emotions were roused in the latter part of the nineteenth century when evolution was a subject of bitter controversy. Here is a quotation from one of the leading figures

in that controversy, namely, T. H. Huxley,¹ who, referring to evolution, said: 'One of its greatest merits, in my eyes, is the fact that it occupies a position of complete and irreconcilable antagonism to that vigorous and consistent enemy of mankind—the Catholic Church.' Time has shown how stupid that statement was, but still, it was prejudice of this kind that resulted in muddled thinking and the creation of further antagonisms between religion and science. The Church, however, kept silent, preferring, no doubt, to wait and see whether the new theory was worth examining.² Such prejudiced views are still met even today when the excuse for ignorance is no longer tenable, but the general atmosphere between religion and science is now much better.

It is well to notice the effect of increasing scientific knowledge on some non-Catholic thought, for it has been progressive and unidirectional. Many one-time believers have lost their personal beliefs, or the beliefs of their forefathers, or they have watered down such doctrines as Free Will, immortality, miracles and so forth. In an intellectual atmosphere of this kind of retrenchment the position today has become one of indifferentism to religion rather perhaps than one of direct conflict. A change of emphasis has been brought about and it has created a problem, however, with which it is difficult to deal. We cannot discuss the matter here, but we may point out a few salient features. In a technical age such as we live in, the great success of science and the wonderful achievements of scientists, engineers and technologists often impress people, and we are all subject to it, so greatly, and without them really realizing it, that they adopt an attitude which in effect implies that they think science to be the be all and end all of everything. The only explanation is a 'scientific' one, apparently because it works. Many people who thus so unconsciously 'deify' science, however, also often believe in freedom of the mind, and so, while they will concede their neighbour the right to be religious if he wants to, they disdain to consider religion themselves because they imagine it is all so unscientific. Apparent contradictions between science and religion are then held against religion and believers, while contradictions in science are quietly dropped and forgotten. It seems that indifferentism is in large

¹ 1893, vol. 2, p. 147.

² It is important to distinguish here between the corporate teaching Church and individuals within it who may give their views.

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measure due to ignorance, but also to a successful, if also culpable, ignorance, and that may be why it is so difficult to counteract it.

4. THE POSITION OF BIOLOGY INCLUDING EVOLUTION

Biology, the science of life and of living things, is today a well-developed science. Its complexities have caught the imagination of men and women of all kinds and conditions who hold a wide variety of fundamental beliefs, or who hold none at all. At one extreme there are those who know no laws but 'scientific' laws and who consider that biology can of itself provide, through evolution and other branches, the basis for a system of philosophy and ethics which will serve as a rule of life and conduct for man as a social creature. At the other extreme there are those who, taking biology just as one facet of knowledge, and perhaps not a very reliable one at that, consider that it is merely the study of life and its manifestations with no deeper implications than can be given by the test tube or the microscope. To them the subject has its uses and abuses, abuses against which one must be on one's guard. Between these two extreme views there is a host of intermediate views of the place and value of biology in science, in society and in education. The important point is that the existence of such diverse and fundamentally different approaches to biology makes the study of evolutionary theory of first-rate importance to both biologists and non-biologists alike; because this theory, like true psychology, occupies the border-line between practical, or truly empirical, investigations of biological science and intrinsic investigations which attempt to unravel the meaning of things.

The study of biology in general, and of evolution in particular, opens up a fascinating field which, according to the capabilities of the student, can satisfy both the deeply learned and the less well versed. It is a study which seems endless, for the solution of one problem merely brings others in its train. The complexities of organic nature are truly astounding and are a never-ending source of wonder and inspiration to true biologists. No single biologist can hope to cover the whole field. Many are content to compare some animals or some plants with their likes and to study the conditions under which they live and grow, others will be content to study their structure, others their chemical make-up, or their genetics and so on; but some people attempt to probe into the

very heart of the matter, and by extended speculation in their chosen biological field, they try to fathom how life in the abstract becomes a concrete means whereby living things have their being. In a broad sense, the biologist and of course the evolutionist use both the methods of analysis and synthesis. They can treat their subject matter as a whole and in communities, or they can investigate it anatomically in parts. Thus their methods are both macroscopic and microscopic. The biologist observes, experiments and infers, and so is led to build up working theories which can then be tested and which may lead to further exploration.

The recognition of science as one method of pursuing knowledge and the acceptance of biology as a true science by those who are not biologists has undoubtedly led to much good in fields beyond the control of biologists as such. The study of living things, their conditions of life and the method of their working gives a well-nigh perfect example of how nature brings order out of apparent chaos by dovetailing a complicated array of individual living things, each possessing its own ends, into a complex but integrated whole which can be made to show an ever-increasing development in the pattern of life. Thus biology seems to present the apparent contradiction of a chaotic orderliness in nature, just as physics teaches us about the orderliness of atoms in a molecule which individually all the time are performing a completely disorderly heat motion which is unceasing.¹ Nowhere in biology is this shown more than in evolution, where nature would appear to progress in an orderly array of forms while the means by which this progress has been brought about would apparently seem to be random, with few or no rules behind them. An extraordinary feature of organic nature is its amazing multiplicity of forms and conditions under which they live; the heterogeneity of nature emphasizes the success of life. Thus biology and evolution give us a picture of nature which demands an 'artiste' to assemble the blobs of paint and blend colour into colour. The biological picture can lead its admirers further afield to consider that there are other rational arguments to explain it besides the biological. And it is reasonable that the very complexities of biology and evolution should lead to a transcendent view outside the biological field. Just as admiration of a great

¹ Schrödinger, E., 1951, p. 8.

picture leads us to admire the artist ever so much more, so also a true appreciation of the glories and wonders of nature may lead us to admire and adore God, the Creator of it all. Many people are not impressed by this type of teleological argument. They say that it breaks down because nature is so imperfect in many of its features, and that the law of the jungle is not very impressive. There is, after all, a reason for the law of the jungle and for all we know the misfits may have a good purpose. Many people, however, are impressed with nature and find it a continual source of inspiration, either as a means to earn their living, or as a means to an appreciation of higher ends, or both. And this fact alone flouts the critics.

The term 'evolution' is now a commonplace, and most people have some acquaintance with it and with its meaning. At the same time there is still a great deal of confusion among some people about the factual content of organic evolution and its interpretation. The empirical aspect of organic evolution is a matter for biologists and their discussions and controversies may have little intelligibility for the layman. But the meaning a person may take out of evolution, i.e. the attempt to find the significance, if any, of evolution for man himself, may lead to an attitude to human life and living which embraces philosophy and morality, and which may influence a person's approach to his Creator. It is possible then for a person's evaluation of evolution to have far-reaching effects on his behaviour and on his destiny. The strict interpretation of evolution in a purely scientific sense has no necessary bearing on philosophy, ethics, or morality, any more than fundamental theories in chemistry have when considered within their own field. It is only when this idea of scientific evolution is applied to human beings, first as members of the animal kingdom, and secondly as rational creatures, that it assumes a great and added importance.

Hence it comes about that a materialistic interpretation of evolution of necessity differs from the Christian approach although the factual content of the theory may remain the same. Unfortunately, it is the materialistic side which has in the past been given most emphasis, often with the aim of weakening the Christian position. The scientific findings of Christian biologists can be turned to the advantage of anti-Christian forces in such a way as seemingly to give the importance of scientific necessity to

their claims. As early as 1894 Weismann was writing that the Darwinian theory should be accepted not so much because there was a *prima facie* case for its acceptance, but rather because it excluded (or seemed to exclude) any design in nature. From scientific evolution there can arise an evolutionary philosophy, and by a false extension, an evolutionary ethic, which may determine a non-Christian's outlook on morality, and if allowed to permeate Christian thought may subtly undermine Christian belief.

The word 'subtly' above was used deliberately. Wood Jones¹ maintained that the rise of the mentality which induced the tragedy of 1914, and later Nazism and its evil excesses, could be traced in great part to the effect of a certain type of Darwinian teaching of the latter part of the nineteenth century. It would be comparatively easy to trace some of the present irreligion, or indifference to religious ideas, or the spread of materialism even among many so-called Christians, or the appeal of atheistic communism, to the development of a mode of thought which invidiously turned Darwinian teaching to its own ends with the help of a fatalistic and too trusting interpretation of modern theories of heredity. Darwinism contains much that is true, but some doubtful implications of the theory when applied without reservation to man, and used as a basis for his behaviour in society, can very easily be made to appear like sound scientific sense. Darwin himself never imagined that his teachings could have such long-term disastrous effects, neither did many of those who embraced his theory and applied it too whole-heartedly to various branches of knowledge. It is acknowledged nowadays that one need only mention the word 'science' to many lay people and they will believe anything given to them, whether it is true science, pseudo-science or non-science.

The theory of evolution attempts to describe an historical process which it asserts has taken place in the world of living things. In essence, and without committing ourselves to a rigid definition at present, for we will find that evolution has many meanings, we may say the theory maintains that, in the course of time, the original living things on the earth have given rise to different living things; that an original few simple organisms have quickly or gradually changed or evolved to produce the manifold

¹ 1939, p. 23.

diversity of organisms we see in the world today. This is the meaning given to it by Darwin and it will serve as our working definition. Evolution then represents a progression from simplicity to complexity, or as it may be technically expressed, from homogeneity to heterogeneity. The evolutionist, as a scientist, seeks to explain how this process has taken place in the past and is taking place now. As a scientist, he first of all assumes that the aim of natural science is to interpret natural events in terms of natural causes. The scientist is not concerned with extra-natural or with super-natural causes of events; these lie outside his domain and he is not equipped to deal with them. This does not mean that the scientist must be opposed to explanations beyond the realm of science; in fact his co-operation is earnestly to be desired in so far as he can give it. Some people seem to be naturally sceptical, others seem to be naturally credulous.

A very good example of more or less organized co-operation of scientists and the Church is seen when a cure takes place at Lourdes. The patient is seen and examined by the President of the Medical Bureau and other members and by his own doctors and again after prescribed times. The documents are seen by the Medical Bureau, The Medical Commission (composed of Catholic French doctors), a Canonical Commission and lastly by the Ordinary.¹ No doubt the method of enquiry could be improved but, considering all the difficulties appertaining to a cure and the probable lack of money, it still serves as a good example of co-operation. Examples like this also emphasize the fact that the scientist is concerned to give a natural explanation, or assign a natural cause, to natural events. This is a very important point which all Christian students of science should constantly bear in mind. It is the basis of their empiricism and of their scientific methods, and it is a most valuable point provided it is not allowed to over-step the mark and concern itself with religious truths such as, for example, the reality of miracles. It is worth noting, as L. Bright² said, that when a scientist is convinced of a miracle 'he has understood it as a religious man, who can read the signs of God'. The recognition of the 'naturalness' of science and the 'transcendence' of revealed religion should really help scientists in general to attempt to achieve a synthesis between their scientific ideas and

¹ For a good short account of procedure at Lourdes see A. T. MacQueen, 1958.

² 1958.

their religious beliefs, by enabling them to see how genuine events in the scientific field fall into line with, and so do not oppose, dogmatic teachings of the Christian Religion which are dogmatic because they are unalterably true.

This causative part of natural science forms its mechanistic aspect, and it must be clearly distinguished from the deeper interpretative aspect which may become philosophical and thus to a certain extent speculative and open to opinion and imagination. The biologist, like any other scientist, is bound to follow the mechanistic line so long as he is dealing with purely scientific or empirical problems. He would be acting illogically if he did not do so. Hence the evolutionist does not admit that evolution is a miraculous process, and in his strict methodology he will not discuss teleological arguments unless forced to do so. As soon as he leaves the strict empirical field, however, he may have to consider these arguments. It is sufficient to state here that this scientific attitude, of course, springs from the dichotomy of thought created by the philosopher Descartes, by the developments of Hume, Locke and other philosophers, and also by Kant's rejection of teleology in the natural world, which have influenced scientific thinking ever since. The biologist having decided to proceed along this path begins in the scientific manner to make his observations, etc., and eventually he arrives at a theory, which in our case is the theory of evolution. This theory is opposed to another theory of special creationism which contends that the larger groups of organisms have not evolved but were created directly by God. This is a speculative theory which does not use the methods of science. It is philosophical rather than scientific, and, in the extreme sense, it assumes that the Creator intervenes in a miraculous manner in the creation, or initial production, of each new species. There is no compelling motive, except that dictated by our reason and inclinations, why a Christian should accept either theory.

It is, of course, possible that both evolution and special creationism together may account for the state of living objects as we know them. It is always possible that the larger groups of plants and animals were specially created. Biology is not really in a position to prove otherwise because the demarcation between the various phyla, as they are called, is clear and distinct and too large to be accounted for by evolution on the basis of the available

data. Their connection by evolution is really assumed by a process resembling extrapolation. Special creation of plants, animals, or of the body of man, is not a dogma, or even part of the teaching, of the Catholic Church. It is, in fact, now clear that the Church encourages the proper investigations of the scientist on the topic of evolution, including that of man's body. She requires only that arguments on the matter be conducted by those qualified to conduct them, and that they should be carried out in a spirit of charity. As far as man is concerned Catholics at any rate are required by Faith to hold that the soul of every individual human being is a distinct creation by God.¹

Many Catholics have opposed evolution. For instance, Sir Arnold Lunn² in a series of articles condemned what he called mechanistic evolution. As we have already pointed out evolution is necessarily mechanistic. What he meant, of course, was materialistic evolutionism which is a materialistic philosophy derived from the scientific theory of evolution. This form of materialism does not follow of necessity from evolutionary theory; it is formulated according to the predilections of the writer concerned. Mr. Douglas Dewar³ also attacked evolutionary theory. He accepted many of the facts as biologists see them because he is a biologist himself, but he interpreted them differently. These writers and others like them, however, are really opposing the whole historical trend of biological ideas as we hope to show later on, because the idea of organic evolution permeates modern theoretical biology in a way that few scientific, or even philosophical, conceptions have done in any comparable branch of thought. Evolution in fact is so thoroughly immersed in biology that biologists take it for granted and scarcely ever discuss the evidence in its favour, except those who are specialists in the matter and who discuss the mode of the origin of species. In a similar way the doctrines of the Resurrection, or of the Incarnation, are so integrally a part of Catholic Faith that ordinary Catholics do not discuss them and similar matters, although, of course, specialists do.

A number of other Catholic writers have opposed the basic principles of evolution on philosophical or theological grounds. The professional practice of these people is to examine any

¹ Pope Pius XII, 1950.

² See Bibliography, various publications.

³ 1934-35.

scientific or other theory which has any bearing on human affairs for it is their duty to find the metaphysical bases of reality. They must examine the principles of any far-reaching scientific idea. As regards evolution, the matter is obviously *sub judice* as far as they are concerned because some theologians and philosophers support the theory while others oppose it. To them the theory presents a subject for debate and consideration; the layman should not be unduly upset if he comes across some Catholic theologian or philosopher who seems to condemn evolution outright. It will be just a personal opinion—as discussion proceeds the same person is quite free to be convinced otherwise. Opinions of this kind should never be confused with the authoritative teachings of the Church. If all theologians and philosophers found the theory, or any other, to be harmful then that would be an entirely different matter, but even so, legitimately qualified people would still be able, indeed it may be their duty, to pursue their researches. As far as scientific theories are concerned new evidence may be forthcoming at any time. It is a very significant fact to note that in spite of all the violent polemics which have been written for and against evolution since 1858, the Papacy only mentioned it for the first time directly in 1950, that is, nearly a hundred years after Darwin brought out his theory.¹ The mention made then was really encouraging and anticipatory. The views of the serious critics of evolution will be dealt with in more detail later.

The reason for the modern position of evolutionary theory is that it works; by means of it biology has been unified, and order has been brought out of chaos. It is not because the available evidence *proves* the occurrence of a complete form of evolution beyond any doubt, because this evidence, except in limited fields, is largely circumstantial—but it is cumulative and impelling towards the one conclusion, namely, the existence of an evolutionary process in nature. It is not because evolution can be used by materialists to attack religion, although that would account for some of its popularity. The evolutionary theory gives a magnificent example of the workings of a most elaborate, complex, but dovetailed system of secondary causes. This system is geared towards one end, that of perfection, and towards Man as the highest attainment of the natural order. Thus

¹ Pope Pius XII, 1950.

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theology, philosophy and biology all give the same conclusion regarding the uniqueness of the end product of nature. St. Thomas affirms that we must first look for the actions of God through natural secondary causes when we are dealing with natural phenomena. The study of evolution leads to a study of secondary causes at the highest level of abstraction excluding the study of man; when man is included a higher synthesis still is attained which may lead to the conclusion that biology too demands a First Cause.

Chapter II
Outline History of Evolution

In this chapter, which will serve as an introduction to the more scientific part of the book, it is intended merely to give a very short survey of the development of evolutionary ideas, except for the particular theory of evolutionary causation known as Darwinism which will be dealt with in some detail. All we wish to accomplish in this outline is to show that an idea of evolution was appreciated long before the time of Charles Darwin. There are not many detailed modern accounts of the history of evolution but the reader may consult Fothergill,¹ Osborn,² and to a lesser extent Singer³ and Nordenskiold.⁴

Many people mistakenly suppose that evolutionary theory began with Charles Darwin. In point of fact some of the ideas of the Ancient Philosophers are best described as evolutionary. These philosophers sought to give an explanation of the world and of living things and some of their explanations and reflections suggest an appreciation of a fundamental feature common to all matter, that is, the notion of change. We know now that biological change is evolution, although the Early Thinkers did not realize it as we do today. For descriptive purposes it is simpler to treat of the development of evolutionary ideas and theories in periods,⁵ and for our purposes here we may recognize four periods as follows: (a) the early period; (b) the speculative period; (c) the formulative period; and (d) the modern period. The most important features of the modern period will be dealt with separately in detail under the general title of 'Modern Evolutionary Theory' (see Chapters 3-6).

I. THE EARLY PERIOD

Ancient philosophers, whether Chinese, Egyptian or Grecian, had quite definite ideas about the origin of things. The Chinese

¹ 1932.

² 1924.

³ 1921, 1941.
⁶ See Fothergill, 1932.

⁴ 1929.

conceived of five primary elements—water, wood, fire, soil and gold which existed at the beginning, and life arose out of these primary stuffs through their interaction.¹ Thus life was considered to arise spontaneously from things of a completely different nature and order. To Confucius and his followers the word *Yi* meant some kind of change in the natural world, a change from simple to complex. The Taoists used the word *Tao* to convey the same idea. In 700-600 B.C. Confucius taught in his *Yi-Chang* that things were 'originated from a single simple source through gradual unfolding and branching'.² This is surely a very old saying with a very modern ring about it.

Ideas of origin held by the Ancient Egyptians may be found expressed in the *Legend of the Creation*³ where we see that *Khephera* was thought to be the Creator of all things and *Nu* was the abyss of water out of which *Khephera* raised up all living things. Man originated from the mind of the Creator in seven distinct stages. Here then was visualized a process of evolution by stages, which were potentially in the mind of *Khephera*. Similar ideas may have been echoed by St. Augustine of Hippo in his thoughts of the potentiality of creation and evolution of things.

The Ancient Greeks, like the Chinese, also wrote of primary elements. The Ionian Thales thought that water was the primordial element. Empedocles and other Greek writers, however, recognized the four elements, earth, air, fire and water, with their respective qualities of dry, cold, hot and wet. Aristotle developed these ideas further by considering the contrarieties which could not exist together in one body, for example a body could not be both hot and cold, or wet and dry, at the same time. But each of the four primary elements may be made up of two primary qualities, for example a body may be hot and then cold. Empedocles has been called the 'father of the evolution idea' by Osborn, and indeed he taught a kind of evolution in that he considered life arose gradually through an unconnected series of imperfect forms. At first these forms were ill-adapted to live and reproduce themselves, but they became adapted later. They were formed in the order plants, animals and man. Other ancient Greek thinkers, such as Anaxagoras, Heraclitus, Democritus, Diogenes, etc., held ideas which also contained the germ of an

¹ See Tye Tuan Chen, 1929.

² Tye Tuan Chen, 1929, p. 50.

³ See Dudycha, 1932.

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idea of change and development, or of spontaneous generation; but all of these ideas were purely materialistic.

A true philosophy of change was probably first developed in detail by Aristotle, the pupil of Plato. Aristotle is generally regarded as primarily a philosopher; indeed he is often called 'The Philosopher' by St. Thomas Aquinas. But it should be remembered that he was also an accomplished naturalist and he probably had a good first-hand knowledge of many living things. His chief book in this regard is the *Historia Animalium* which contains a wealth of biological observations and facts. Other books of a scientific or biological kind include the *Physica*, *De Partibus Animalium* and the *De Generatione Animalium*.

The *Historia Animalium*¹ is an amazing book when we consider that it was written three centuries before Christ. Aristotle, however, superimposed his theory of hylomorphism, or of matter and form, on the more naturalistic views of the earlier Greek philosophers. Osborn² says that Aristotle taught an evolution from 'polyp to man'. And in fact Aristotle's treatment of animals in his history is so detailed that an excellent classification of them may be compiled from it. Aristotle thought that things were produced in a sequence of perfection in the order: lifeless, plant, animal, man, which suggests that he had definite ideas of evolution. But there are many objections to this suggestion. In Aristotle's view it is the order of perfection which evolves rather than the things arising in this order. The theory of matter and form may be too rigid a concept to allow change of one form into another. Individuals may die, or change, but the species is immutable.

The account of the Creation given in Genesis sets forth the beliefs of the Jewish people. Here also God creates the universe out of nothing and living things appear in a definite order which is also an order in the scale of perfection ending finally with man.

Hence, many ancient philosophers based their philosophical ideas on the existence of 'primitive stuffs', such as earth, air, fire and water, or on a 'boundless void', out of which all things came by some process of unfolding. They concentrated on the idea of 'becoming' by stages as an ordered progression of change from simple to complex, or from less perfect to more perfect. Evolutionists could express the same idea by saying that the change is from homogeneity to heterogeneity. Change seems to

¹ See Fothergill, 1952, Appendix 2, for a concise account.

² 1924.

be a fundamental feature of the scheme of things but it is so familiar to us nowadays that we tend to overlook it. Nevertheless attempts at an analysis of change have persisted from the very earliest times up to our own day and we cannot say that its possibilities have yet been fully explored. The idea of change lies at the basis of all evolutionary thought—the change of one species into another species by natural means. Without change there could be no evolution, and there would seem to be an historical continuation of thought in this respect from Confucius to the present time. This is clear enough, but it is important to appreciate it because it explains why evolutionary theory may be used as a bridging theory connecting philosophical and empirical facts and ideas. It follows that any explanation of evolution which does not take account of both the philosophical and the scientific aspects is at best only a partial explanation.

2. THE SPECULATIVE PERIOD UP TO ABOUT A.D. 1790

Aristotle's influence extended up to and into the Renaissance period when a new type of biologist developed who investigated biology for its own sake and not because it formed a part of philosophical speculation. In this speculative period we encounter men called the Naturalists like Ray, Tournefort, Linnæus and Buffon who classified organisms and invented systems of classification. The greatest of these classifiers was probably Linnæus. At first their classifications were simple and purely arbitrary, such as a classification of plants into trees, shrubs and herbs. But they ended by becoming highly organized and complex arrangements such as the sexual and binomial system of Linnæus on which many modern systems are ultimately based. Linnæus began with the belief that species were immutable but he ended by thinking they were mutable.

These Naturalists, or Classifiers, investigated resemblances and differences between different species of plants and of animals. Their efforts to group organisms reflected a desire to find the natural classification corresponding to their true connections in nature. Thus, they also seemed to be striving for an over-all explanation of why living things could be placed together into the various categories such as classes, families, genera, etc. They did not find an explanation because their knowledge of external

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nature was not then detailed enough to allow them to do so. They did, however, gradually come to realize that change in a species could occur, but they did not really envisage any genetic or blood connection between different species. The discovery or realization that species could change, however, was of supreme importance in biology and it laid the foundation of all subsequent work concerned with the interrelationship between organisms. Hence, without the laborious and patient work of these Classifiers later progress could not have been made. The Naturalists were also probably prevented from penetrating deeper into reasons why organisms may be assembled in a natural classification by lack of appreciation of the differences between homology and analogy concerning the parts of animals and plants. An understanding of these two distinct concepts was only to come in the nineteenth century.

During this period the so-called Natural Philosophers such as Bacon,¹ Descartes, Leibniz and Kant were also very active. We do not need to describe the work of these men but it is necessary to indicate how they affected the trend of evolutionary development. The Natural Philosophers recognized clearly and distinctly that change in the world of living things was a fundamental feature and this recognition eventually led Kant to formulate a definite idea of evolution in precise terms. Thus, these philosophers were in advance of the Classifiers in this respect. In order to make this advance the Natural Philosophers found it necessary to create a dichotomy, that is, they separated what may be called mechanism from vitalism. Such a fundamental distinction enabled biologists to proceed with their scientific investigations unencumbered with any necessity to consider the 'vital principle' or 'soul' of living things and to ignore final causes. This achievement of these philosophers was a great advance in thought at the time and it probably gave *direction* to the *course* of science by giving a new emphasis to natural causation in a tendency to see natural events as primarily, if not completely, the result of natural causes. We must not think, however, that before this period natural causation was not properly understood by philosophers. It was, but Cartesianism and the systems of the other Natural Philosophers emphasized secondary causes and so produced a

¹ Bacon, of course, preceded this period but he is generally recognised as the first of the Natural Philosophers.

shift in the mode of thought which, of course, persists up to the present day, although many people are coming to realize that the disadvantages of the original dichotomy may outweigh its advantages, for eventually this dichotomy in philosophy led to Hume's denial of causation. The Cartesian dichotomy eventually gave rise to the principle that teleological explanations were not necessary in biology and so Kant was able to reject teleology in order that study of nature could proceed on experimental and mathematical lines.

The result was that empirical science, or what soon came to be called simply *science*, could now give a sufficient, if not wholly complete, causal explanation of phenomena. However, the recognition of mechanism gave a great impetus to the development by philosophers of the idea of an evolution of living things and this period ended with Kant, who for the first time and on the basis of his philosophical speculations gave a positive and unequivocal statement of the possibility of genetic evolution, i.e. of a blood relationship, from man down to the polyp, then to plants and finally to inanimate matter. The modern idea of evolution is a direct extension of Kant's philosophical views and these views at the time gave the philosophical explanation of the work of the Naturalists with their plant and animal systems of classification. We quote the relevant passage from Kant.¹ After discussing some facts of comparative anatomy and morphology Kant wrote:

This analogy of forms, which with all their differences seem to have been produced according to a common original type, strengthens our suspicions of an actual relationship between them in their production from a common parent, through the gradual approximation of one animal genus to another—from those in which the principle of purpose seems to be best authenticated, i.e. from man, down to the polyp, and again from this down to mosses and lichens and finally to the lowest stage of nature noticeable by us, viz., to crude matter. And so the Technic of Nature, which is so incomprehensible to us in organised beings . . . seems to be derived from matter and its powers according to mechanical laws (like those by which it works in the formation of crystals).

Just as the ancient philosophers had vague ideas of evolution to a certain extent independent of their knowledge of natural history,

¹ See J. H. Bernard's trans. of *Critique of Judgment* (1914), p. x, Append. Sect. 80, pp. 337-338 and p. 418.

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so now we see that the first definite statement about genetic evolution was given by a philosopher in advance of the biological knowledge of his time and not by a biologist, although Kant in fact started his career as a scientist.

3. THE FORMULATIVE PERIOD FROM A.D. 1790 TO 1901

The formulative period in the history of evolutionary thought may be said to begin about 1790 after Kant's enunciation of the principle of genetic affinity. This period is a long one reaching up to the beginning of modern evolutionary ideas when the work of Gregor Mendel was re-discovered by Tschermak, Correns and de Vries in 1901. Evolutionary matters were brought to a head during this period when Charles Darwin launched his theory of natural selection and integrated evolutionary evidence. The discoveries of this period follow in logical order from those of the previous period, but there was a definite change of emphasis. True, biologists still continued to classify organisms and the binomial system of Linnæus bore fruit by reducing the labour involved in the description of species and allowing a 'philosophy' of classification to emerge. Hence, biologists could now turn their thoughts away from mere classification for classification's sake into deeper channels attempting to elucidate the reasons why biological organisms are classifiable in a so-called Natural System.

We do not wish to give a detailed account of the discoveries and thought of this period,¹ but it is necessary to mention a few of the major features of the period until we come to Charles Darwin when a more detailed account of his theory of evolution will be given.

The period begins with Erasmus Darwin, the grandfather of Charles Darwin, who was a naturalist with many speculative ideas about things in general.² Erasmus Darwin certainly seems to have had quite definite ideas of the evolution of living things and he also believed in the inheritance of acquired characters.³ Many of his evolutionary beliefs were expressed in the form of poetry which is sufficiently unusual to merit mention.⁴ However, in the

¹ The reader may consult Osborn, 1924, or Fothergill, 1952.

² A good biography is by Hesketh Pearson, 1930.

³ See *Zoönomia*, 1794-96. ⁴ See *Temple of Nature*, 1803.

early part of this period the outstanding biologist was Jean Baptiste de Lamarck who really initiated the modern approach to evolution from the biological side.

We have already seen that many of the ancient philosophers concentrated on the ideas of 'being' and 'becoming', or on 'change' which they recognized as fundamental features of reality. From the time of Lamarck, modern evolutionists have been more concerned with the idea of 'becoming' or with change itself, rather than with the metaphysical idea of 'being'. Thus biologists began to concentrate on the fact of, and the reason for, change in organisms, that is, they concentrated on the genetic continuity of natural species which were by that time considered to be mutable. Such naturalists as Buffon, Lamarck, Geoffrey St. Hilaire and others had in fact given up the belief that species were immutable or specially created. The only experimental way by which the nature of the mutability of species can be studied is by the investigation of small-scale changes between them, or between smaller units within a species. The rational foundation for this method of attacking the problem probably lies in the common-sense attitude that if we learn how the several parts of a process work individually, we shall ultimately come to a realization how the process itself proceeds. Thus modern evolutionists work on the anatomy of evolutionary processes.

Lamarck had a very wide knowledge of natural history and when he became professor at the Paris Museum of Natural History he turned his attention to a re-classification of animals, particularly the invertebrates, or backboneless animals, and then later he became interested in the 'philosophy' of zoology.

Lamarck supposed that some animals were less perfect than others, a fact which he considered to be demonstrated by the differences in complexity of the organization of their bodies. He postulated that environment had a great effect on species and caused them to change. If the environment changed then he thought the species would change also. By examination of animals of increasing complexity, i.e. of increasing perfection, Lamarck inferred that species had been produced successively from the worm upwards. He considered that there are no real breaks between species in nature, that is, that there is a continuity of form and organization among species. Such breaks as seem to exist in nature are really due to our lack of knowledge of species.

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Lamarck thus concluded that a biologist should be able to construct a natural classification. To Lamarck species were connected in classification and in nature in a straight line fashion, that is, linearly, and not reticulately, as modern classifiers connect them.

It should be noted here that Lamarck clung to the old Aristotelian notion of perfection. But this is not considered to be a scientific term because one can hardly measure perfection or imperfection. In its own way, and in a biological sense, a tapeworm may be just as perfect as the dog in which it lives, although, in any scheme of evolution, these animals would be far apart. Perfection is a philosophical term and may enter into the interpretation of evolution but not perhaps into a consideration of the process itself considered mechanically. Nevertheless, the ideas of complexity and perfection considered in relation to the environment enabled Lamarck to build up the first really complete theory of evolution in his book *Philosophie Zoologique* published in 1809.¹ Thus Lamarck pre-dated Charles Darwin by fifty years and his theory came to be known as Lamarckism.

Lamarckism, at least superficially, is a very reasonable and commonsense theory with a wide appeal. According to the theory a species modifies itself as a result of the cumulative inheritance of the effects of its constituent individuals. Lamarck did not invent this idea because it was tacitly assumed at his time and had been so for centuries before as Zirkle² has shown, and indeed, is still so today. But Lamarck developed this accepted idea logically.

Stated as concisely as possible the theory depends on two laws: (a) the law of use and disuse, which involves the striving of the species towards something better suited to its surroundings, and (b) the inheritance of the characteristics acquired during the lifetime of the organism. The first law is simple and straightforward—it means that if an organ is used it will be developed further, or evolve; if it is not used it will become atrophied and lost. But Lamarck introduced a mystical element at this point by conceiving the species as striving towards perfection. The second law, however, became the really controversial part of the theory and it was also thought to be more susceptible of scientific investigation.

¹ See English trans. by H. Elliott, 1914, London; and his biography by A. S. Packard, 1901.

² 1935, 1936.

The theory of the inheritance of acquired characters has in fact been hotly contested since the days of Darwin. Lamarck himself never bothered to test his statements experimentally. In essence Lamarckism does not contradict, or stand opposed to, Darwinism, although it is often made to seem so. Many of the examples which Lamarck used to illustrate his theory were purely fanciful, such as, that snakes have lost their legs because they have to pass continually through narrow places where legs would be a nuisance to them.

In modern times serious experiments have been carried out to show that acquired characters may be inherited. Most of these experiments have failed in their object and some are doubtful, such as those of W. McDougall¹ on rats, J. W. H. Harrison¹ on the sawfly and D. B. Sladden and H. R. Hewer¹ on *Caranaria*. The investigations of these people may show the inheritance of acquired characters but their results, and those of similar experiments, may often be interpreted in other ways and biologists generally do not seem to agree with a Lamarckian interpretation. Confirmation of such experiments is often very difficult to obtain. Yet, even if these experiments have failed in their immediate objectives, Lamarckism is not thereby disproved; all that would be known is that these experiments did not furnish indisputable proof of the theory. Lamarckism as a theory has been neither proved nor disproved, but it seems that the weight of the evidence is against it rather than for it. On the other hand, many biologists, without perhaps saying so expressly, seem to believe in it; at least biological literature contains many examples of Lamarckian ideas and interpretations.

While a critical re-evaluation of the position of Lamarckism is long overdue—at least one modern biologist has striven to do this²—there are still many reasons for the present attitude. One of them is possibly a dislike of the idea of perfection which permeates Lamarckism, and which many scientists eschew because of its philosophical implications. Again, in a sense, Lamarckism has been forced out of the biological field by the dominance of the neo-Darwinian theory of natural selection which is considered to

¹ McDougall, a series of papers beginning 1907 and ending 1937; Harrison, 1927; Sladden and Hewer, a series of papers beginning 1934 and ending 1938; for detailed account of the experimental evidence for Lamarckism the reader may be referred to Podbergil, 1932.

² H. Graham Cannon, 1938.

be a purely biological theory making no appeal to philosophical ideas. The position may be summed up as follows: Lamarckism at present, in spite of its commonsense appeal, seems to be incapable of rigid scientific analysis. The Lamarckian method of evolution is possible: it may or may not be true. H. Graham Cannon¹ is strongly of the opinion that evolution depends not on genes ("the playthings of the Neo-Mendelians"), but on some inexorable physico-chemical law inherent in organisms—and perhaps this is what Lamarck was really attempting to teach under the guise of perfection. Cannon does not think that his views are in any way materialistic. It is possible that the general attitude towards Lamarck's views may change—for example, Waddington² finds it necessary to speculate in the Darwinian-genetical method rather deeply in order to explain the appearance in descendants of a structural modification produced in the parents by an external stimulus and selected for breeding experiments, even when the stimulus is no longer operative.

Lamarck died in 1829. Elsewhere we have written³ 'As a biologist he stands as one of the greatest men of his time; his contributions to systematic zoology alone entitle him to the greatest respect. He was the real founder of evolutionary theory, and by his theory of the inheritance of acquired characters he founded a school which will long have its adherents'.

After Lamarck, biologists such as Geoffrey St. Hilaire, Owen, Goerke and others slowly began to realize the existence of an evolutionary process in nature. In 1844 Robert Chambers published his *Vertiges of the Natural History of Creation* anonymously. This book became very popular and went through twelve editions. In it evolution was recognized as a process in nature occurring through natural means. During this period, after the time of Lamarck, paleontology came into being as a serious study through the works of William W. Watts, Sir Charles Lyell, Cuvier, Owen, Agassiz and others. As the number and kinds of fossil plants and animals accumulated and their significance became realized, it would have been incredible if a conception of evolution had not arisen among biologists and paleontologists, but it was really left to Charles Darwin to crystallize the evidence in this regard.

In the next section we deal with Charles Darwin and Darwinism

¹ 1958, p. 169.

² In S. A. Barnett, 1958.

³ 1952, p. 77.

but first we should point out that shortly after Lamarck died the foundations of what is called the *cell theory* were laid by Schleiden and Schwann in 1838 and 1839. The importance of this theory is that in it the cell was recognized as the primary agent of organization of the plant or animal body. Once the cell was thus recognized as the unit of living things, the way was clear for further fundamental developments leading to the modern science of cytology. Cytology is the study of the cell which includes the study of chromosomes and their behaviour, and without a knowledge of these bodies there could hardly be a true causal theory of evolution as we have today. Beyond mentioning the discovery of the cell theory there is no need to develop the matter further. It will be necessary later to give an account of cell division and chromosomes (see Chapter 5).

4. DARWINISM

Sir J. E. Smith bought the books and manuscripts of the great botanist Carl Linnaeus after the death of the latter's son in 1783, and brought them to London. A few years later in 1788 Smith founded the Linnean Society of London which became incorporated by Royal Charter. In 1828 he gave Linnaeus' books and other botanical effects to the Linnean Society for their preservation. Since then this society has functioned as one of the great botanical societies of the world, publishing journals of its own. In 1908 the Linnean Society met to commemorate the jubilee of a famous meeting held on 1 July 1858 at which Charles Darwin publicized his evolutionary theories for the first time. At this commemorative meeting Dr. D. G. Scott, the President, said: 'We are met together today to celebrate what is without doubt the greatest event in the history of our Society since its foundations. Nor is it easy to conceive the possibility in the future of any second revolution of biological thought so momentous as that which was started fifty years ago by the reading of the joint papers by Mr. Darwin and Mr. Wallace.'¹ This is a startling statement when we realize that it was made by an outstanding and gifted botanist not given to the use of superlatives. In 1858 a great biological event occurred which changed the whole science of biology just as Einstein's Relativity theories and Max Planck's

¹ 1908, pp. 1-2.

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Quantum theory, or the application of nuclear energy, are now ushering in a new era.

Charles Darwin was born at Shrewsbury in 1809. He was the fifth child of Robert Waring and Susannah Darwin, and was the grandson of Dr. Erasmus Darwin who was a prolific and fascinating writer on many subjects and whose biographer said he was 'the man who gave a creed to Creative Evolution'.¹ In 1825 Charles Darwin went to Edinburgh University and later in 1828 he entered Christ's College, Cambridge. He studied medicine at Edinburgh but found both his lectures and his teachers incredibly dull. His intention at Cambridge was to become a clergyman. He tells us that he had no scruples about believing all the dogmas of the Church of England, and at that time he accepted every word of the Bible as literally true. He also wrote: 'Considering how fiercely I have been attacked by the orthodox, it seems ludicrous that I once intended to be a clergyman. Not was this intention and my father's wish ever formally given up, but died a natural death when, on leaving Cambridge, I joined the *Beagle* as Naturalist'.² He did not particularly distinguish himself while at college, but he obtained his degree in 1831. During his later undergraduate days and for a while afterwards he became friendly with Henslow, the professor of botany at Cambridge, and also with Professor Sedgwick, the zoologist. In the company of these people he developed a taste for natural history. A short time after his graduation Henslow suggested that he should join the *Beagle* as an unpaid naturalist. The *Beagle* was commissioned and sponsored by the Admiralty to travel to South America on a voyage of exploration and charting. Darwin was away for about five years (from 1831 to 1836) and during that time his whole life and outlook were changed. Darwin³ himself summed up this period of his life when he wrote: 'The voyage of the *Beagle* has been by far the most important event in my life, and has determined my whole career. . . . I have always felt that I owe to the voyage the first real training or education of my mind; I was led to attend closely to several branches of natural history, and thus my powers of observation were improved, though they were always fairly developed.' During the voyage he made large collections and studied geology, paleontology,

¹ Hesketh Pearson, 1930, Intro.

² P. Darwin, *Life and Letters*, 1887, Vol. 1, p. 45.

³ *Ibid.*, Vol. 1, p. 61.

botany and zoology. The material he collected and the notes he made during the voyage served him practically for the rest of his life—about forty-six years (he died in 1882)—and gave him the factual basis for his many books and other writings.

During his travels he became impressed with the profusion and variety of nature and natural objects, and he was extremely puzzled by the possible causes of this. His belief in special creationism did not help him. In fact he came to realize that those old views were untenable and stood in the way of any explanation of the varieties and their distribution in the parts of the world to which he had been. He described this change in his outlook in a letter written to Haeckel¹ in 1864 which summarized the beginnings of his theory. He wrote:

In South America three classes of facts were brought strongly before my mind. Firstly, the manner in which closely allied species replace species in going southward. Secondly, the close affinity of the species inhabiting the islands near South America to those proper to the continent. This struck me profoundly, especially the difference of the species in the adjoining isles of Galapagos Archipelago. Thirdly, the relation of the living Edentata and Rodents to the extinct species. I shall never forget my astonishment when I dug out a gigantic piece of armour like that of the living armadillo.

By 1844 Darwin had become convinced that species were mutable, that is, that related species were descended from one ancestral form, but had changed during their descent. In other words, he put what earlier workers called 'affinity', which was largely used in a metaphysical sense, on a biological basis. Affinity meant genetic relationship.

Darwin had read Malthus' *Essay on Population* which contained the germ of the idea of natural selection as it occurs among human beings, and this idea influenced him greatly. Thus, by 1844 he had formulated the central point of his *Origin of Species*. He showed his notes (about two hundred pages) to Hooker, the botanist, and to Lyell, the geologist. For the next twenty years or so Darwin examined his material and gathered all the evidence he could find to support his theory. But in the meantime Alfred Russell Wallace was in the Malay Archipelago also studying natural history, and he came to conclusions very similar to those of

¹ Letter to E. Haeckel, 8 October 1864, quoted by Haeckel, 1868, p. 119.

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Darwin. In 1858 Wallace sent Darwin an account of a theory of natural selection which he had arrived at. This was an impasse and Darwin put the matter to Hooker and Lyell. The problem was solved by the reading of joint papers by Darwin and Wallace before the Linnaean Society on 1 July 1858. In the following year Darwin's great book *On the Origin of Species by Means of Natural Selection and the Preservation of Favoured Races in the Struggle for Life* was published. This was the real beginning of Darwinism and the response of biologists to Darwin's book was phenomenal.

It is important to realize what Darwin attempted in this book. He set out to do three things as follows: (a) to explain facts of biology with reference to the multiplicity of kinds which he had seen and studied; (b) to establish the fact of an evolutionary process in nature; and (c) to give a causal explanation of how this evolution could have occurred. Darwin was the first biologist to assemble *all* the available evidence pointing to the conclusion that evolution had occurred. It was the juxtaposition of all his lines of evidence, their integration and their strong cumulative effect, which convinced so many biologists at the time (and, of course, today also) of the veracity and existence of evolution. Darwin in fact presented a new method of approach to biological problems, and its advantages were obvious. By making comparisons in an orderly fashion he led biologists to a single comprehensive generalization regarding living things and suggested an historical reason for their continued existence. Lamarck also had generalized about evolution but his conclusions, while valuable in some regards, did not seem to be based on completely satisfactory biological evidence. Darwin's conclusions, however, did give an impression of validity to many of his contemporaries because of the great mass of observable facts assembled to support them. Thus Darwin collected his evidence from different realms of science, from comparative anatomy, from the geographical distribution of plants and animals, from the geological succession of fossils, from embryology and from the classification of species. He used these lines of evidence to connect the ideas of unity of plan and of affinity to which he gave empirical meaning, thus leading to the conclusion that species had evolved from pre-existing but slightly different species. Having shown the fact of evolution, he then explained how the process took place, that is, he brought in natural selection.

A certain amount of recapitulation seems necessary at this point. We have seen earlier in this chapter that a belief in evolution had been implicit in men's minds for a long time. We have seen how naturalists often were not really aware of this belief, that they struggled to formulate it, but could not. These men were held back in their attempts to recognize evolution as a real process in nature possibly to a large extent by a theory which held sway for centuries. We refer here to the theory of special creationism, according to which each species was created just as it is by the Creator. Such an idea of fixity or immutability of species was somehow or other ingrained in the minds of many biologists. Philosophers knew all about change which was indeed a central notion of all ancient philosophies. Ordinary people saw change going on around them. And yet this fixity of species was believed even when no one had any idea what really constituted a species. Special creation of species and all that it implies has never been considered by the Church, and there was little reason why it should be, because it is rather a question for philosophical biology than for theology. We are not certain but it seems that many of the medieval theologians did not have very strong views about the matter. It is possible that the rise of Protestantism with its strong emphasis on the literal and personal interpretation of the Bible, particularly Genesis, may have contributed in large measure to this 'subconscious' hold which special creationism had on people in general and many naturalists in particular. The question, of course, was largely academic, because of the ill-developed state of biology up to the time of the middle of the 19th century.

We are not saying that everyone believed in special creation, for there were naturalists who did realize the dead end they were in because of this theory. It was indeed a paradoxical position. Naturalists knew perfectly well that species were modified in various ways. But if they asked why they were so modified, they were told, as Bentham¹ related, that it was the will of the Creator, or that it was beyond their comprehension. We have already indicated that some naturalists had broken away from special creationism. For example, the following became convinced that species were mutable: Buffon, Erasmus Darwin, Lamarck, Spencer and some others. They had in fact arrived at a theory of evolution. But their ideas never seem to have caught hold of the

¹ 1874, p. 37.

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imagination of biologists in general and they were never integrated. The philosophers knew the answer, indeed they had always had it, and Kant had given the naturalists the clue they all wanted to explain the infinite variety of plants and animals in the world, but few of them took it up until Charles Darwin discovered the connection independently and from biological evidence alone. His solution to the problem was simple and direct. It was a stroke of genius and it consisted just in this; that among species there was *genetic descent with modifications which were naturally selected*. This seems to be stating the obvious now, but few biologists had grasped its significance until Darwin enunciated it. Descent with modification was the key to the understanding and the explanation of the evolution of species. Its enunciation ushered in the biological revolution which D. G. Scott talked about at the Linnaean Society meeting in 1908. One may say that Charles Darwin changed the whole outlook of biologists overnight as it were, and much of modern theoretical biology springs from that simple phrase.

It is necessary to state the theories which Darwin put forward. These theories in their original form became known as 'Darwinism'; later, after a period of decline, Darwinism was resuscitated and was then called 'neo-Darwinism'. Nowadays the original Darwinism is considerably modified, but its basic tenets have been incorporated in the modern theory in much the same way that Mendel's principles form the basis of modern genetics. It is not correct, however, strictly speaking, to call this modern theory either Darwinism or neo-Darwinism. At the present time the modern theory has not got a name which is correctly descriptive of it.

Natural selection is the keystone of Darwinism. With true psychological insight Darwin in fact began his *Origin of Species* by considering the effect of man's selection on races of domestic plants and animals. He concluded that the accumulative action of selection had resulted in improvement of many breeds and had led to production of new ones. His most celebrated example was that of the common or domestic pigeon which exists in so many varieties. He collected varieties from all over the world. And by careful study and breeding of them, he proved that all the various breeds were descended from one single species—the European Rock Dove (*Columba livia*). The influence of human selection in

this way was so clear that Darwin's contemporaries were thus pre-disposed to appreciate his arguments for natural selection.

The term 'natural selection' was a particularly unfortunate choice of words by Darwin to explain what he meant. The phrase 'survival of the fittest', which is far more explanatory, is also used and has not the human connotations which the first phrase has. Darwin himself was careful to point out that natural selection was only a metaphorical expression. Nevertheless the common use of the term and its over-emphasis has led to the belief among many people that nature *selects*. This is brought about by personalizing 'nature' in terms of capabilities towards a conscious choice and by depersonalizing purposive selection towards a non-rational 'choice'. The term 'natural selection' as used in the Darwinian sense is a metonymy, whether those who use it understand its implications or not, because it involves a contradiction. The word 'nature' means the non-rational aspect of the universe, while the word 'selection' means the free choice by a rational person.

It is easy then to argue for an evolution controlled purely by chance, by referring to the work of a non-rational entity as though it were that of a rational creature. To make the position concise and clear this misuse of words in the phrase 'natural selection' must be emphasized because it is rarely mentioned in the Darwinian literature, and unless the meaning of the term is grasped by the mind the interpretation of Darwinism will be coloured. These remarks apply with equal force to some modern evolutionary writings, but in the more advanced type of biological papers there is a tendency to use only the single word selection which is justifiable because the process in nature which is dealt with does simulate selection. We must therefore retain the term here firstly because of the lack of another suitable term and secondly because it is in such common use nowadays.

The argument in favour of Darwin's natural selection theory is based on three sets of facts and two deductions from them. These are given below.

1. *Variation.*

An examination of individual plants and animals shows that types or species can be recognized with reasonable clarity. But individuals are always different from each other, so that the species

is made up of a larger or a lesser number of similar varieties each of which differs from its like varieties in some way. This is a fact of observation. Darwin found that genera with more species showed a greater number of varieties than those genera with a smaller number of species. On the theory of special creationism it would be difficult to find a reason for this, but it is easily explained if it is assumed that species originate as varieties, and later become species.

2. *Over-production.*

Very many plants and animals produce very many seeds or eggs which, if all grew and developed, would soon cover the earth. One of Darwin's examples was that of the elephant which he found starts breeding when it is about thirty years old and lives till it is about one hundred years old; in that time it produces on the average about six young. It is reckoned to be one of the slowest breeders among animals. But even so, after a period of seven hundred and fifty years, there would be nearly nineteen million elephants alive descended from only a single pair. There are many similar examples even more striking—the number of seeds produced by a sunflower or a hollyhock runs into thousands, while some fishes may each produce a million or so eggs. Thus there is much evidence to show that plants and animals tend to increase in numbers in a geometrical ratio.

3. *Relative constancy of numbers.*

Over a period of time the relative numbers of individuals and species, etc., remains more or less constant. Hence many plants and animals must be destroyed at some time of their life, otherwise, due to the large numbers of seeds and eggs produced, the earth would not be large enough to contain them, and this is not so.

4. *Struggle for existence.*

The first deduction from the above facts is a very important one for the theory. If large numbers of individuals are destroyed then it is reasonable to say that there is a struggle for existence among them. Consider, for example, the grasses in a mass of thick turf—it is fairly obvious that there is just not enough physical room for all the seedlings they produce to grow. There is a competition among species but it is not necessarily a conscious

struggle. It is true that two fighting animals may be conscious of their fight, but they are not aware that they may be having an effect on the numbers of their species, or again, Darwin's example of a plant on the edge of a desert is not aware of a struggle against an ever-recurring drought. Seedlings in any tightly packed area will be competing for water. Thus Darwin considered that the struggle occurred between individuals of the same species, or between individuals of different species, or again against the physical conditions of life.

This competition among species has been vividly illustrated in some cases where the normal competition which a species encounters has been removed; opportunity was then provided for the tendency of the species to increase in numbers. For instance, the Canadian waterwood (*Elodin Canadensis*) was introduced into the River Cam and within a very short time it had increased so much as seriously to interfere with the boating on the river, and subsequently it spread in the absence of its natural competitors to many waterways, becoming a serious pest. Rabbits were introduced into Australia and soon increased so tremendously in numbers as again to become a serious pest.

5. *Survival of the fittest or natural selection.*

This is the final deduction and crux of the theory. It is based upon the fact of variation and the first deduction of the struggle for existence. Given these two premisses, then, it follows that varieties with favourable features in a given environment will tend to survive longer than those with less favourable variations. The conclusion is that they will be *naturally selected*. Darwin expressed the argument thus:

As many more individuals of each species are born, than can possibly survive; and as, consequently, there is a frequently recurring struggle for existence, it follows that any being, if it vary however slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving and thus be *naturally selected*. From the strong principle of inheritance, any selected variety will tend to propagate its new and modified form.¹

Darwin considered that this process of natural selection took place automatically. It does seem as though nature 'selects'

¹ 1859, 3rd edition, pp. 4-5.

certain types. It is undoubtedly true that the process does occur, but the advantage of this to the species as a whole is assumed in Darwin's theory and not proved. In a certain environment a certain variation may be selected but the advantages the variety possesses may be unfavourable in another slightly different environment. Thus natural selection acts fortuitously and on the average it could be expected that the normal form of an organism would be perpetuated because it at least has been tried; the variations would cancel each other out in the long run, or their effect would be nullified. It is thus possible that natural selection could lead to constancy, not change; the Darwinian inference, of course, is the direct opposite of this one. Darwinians maintain that if favourable variations are continuously selected by means of natural selection, then through reproduction and heredity such variations will tend to accumulate in the species and gradually come to change it. The function of natural selection is to lead to the evolution of species; natural selection could be said to be the cause of evolution. According to this theory evolution seems to occur by means of a haphazard process. Hence the phrase 'evolution occurs by chance'. Now 'chance' is technically a mathematical word, and as such it does not mean that the operations concerned in it are working against or without known laws.

The reader may well ask here: 'Natural selection may be a fact of nature, but if the favourable variations are small how can they have any effect on evolution?' The question is valid and in fact crucial. Small single variations by themselves would not affect the course of evolution and natural selection would then be just a phenomenon which led to the extinction of misfits. Natural selection only affects evolution under certain conditions: (a) the favourable variations which occur must be inherited; (b) they must be uni-directional because obviously a variation linked to an unfavourable one, or one in a contrary direction, would lead nowhere; (c) they must be cumulative. Hence Darwin postulated the occurrence of slight continuous variations occurring over a longer or shorter period of time and which were continually naturally selected in one direction. As the effect of the new variations accumulated a new species gradually emerged. This would be evolution. Darwin said that natural selection works daily and hourly 'at the improvement of each organic being in relation to its

organic and inorganic conditions of life'. This would seem to indicate only that any approach to perfection of adaptation and fitness attained by any individual, or group of individuals, necessitates a change in the nature of that individual, or group of individuals. In other words, if we assume that the differences separating species are deep-seated, affecting the whole organization of the individuals of that species, and are not merely superficial characteristics, then slight variations continuously occurring and continuously naturally selected may perhaps produce and perpetuate varieties, or races, of organisms but not necessarily species. Some modern Darwinists contend that small variations may under certain circumstances be carried dormant, as it were, in the germ-plasm of a species until a suitable environment gives them the chance of outward expression. Nevertheless, the comments just made are still valid. There is no example of an absolute change of one species into one with a different nature. A *Drosophila* fly, for example, is always a *Drosophila* fly, and as regards members of a fossil series we are scarcely in a position to discuss the *nature* of ancient remains.

Unlike Lamarckism, however, the theory of natural selection is not really a theory of origins at all, because Darwin did not say how the variations arose. He took them for granted (and indeed he could not do otherwise at the time he wrote), and then he supposed that natural selection worked on them. The new species once created represented the sum total of an accumulated mass of advantageous but mysteriously occurring variations. It is interesting that Darwin, like Lamarck, never tested his theory experimentally. This fact is all the more curious when we remember how assiduously he worked on the problem of selection in pigeons and on other matters. He does not seem to have tried to find examples of actual cases of natural selection working in the field. Nevertheless, the theory is an intellectual achievement of the first order, but as a scientific theory it should have had some experimental basis, or at least testing. Even years after the publication of the theory there is not a great amount of experimental work to test it. Just like Lamarckism, it makes several large and gratuitous assumptions. It is assumed first and foremost that the variations Darwin envisaged are inherited. In point of fact what he called variations are perhaps better called modifications which are not inherited; they are probably due to

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minor changes in the local environment. They are distinguished from mutations which are inherited. Hence, if Darwin had tested the inheritability of his variations he would not have been able to give his theory the support which it needed from inheritance. Darwin's variations were imagined as being very small and for them to accumulate in a species they would have to be unidirectional towards the production of some new characteristic appearing generations later. This point also was assumed by Darwin. Again, before the advantageous variations could have any real effect the unfavourable ones would have to be continuously eliminated prior to their reproduction, otherwise they also would affect succeeding generations. And there was no evidence in this connection either. There are other assumptions implicit in Darwinism and in fact a modern writer, J. C. Willis,¹ has enumerated about thirty-three of them, but according to some other writers, such as J. S. Huxley,² not all of them are valid.

One of the outstanding features of the history of biology is the fact that Darwin's theory was seized upon, not only by biologists, but by writers in general. It looked as though the world was waiting for such a theory. Here apparently was a purely natural explanation in terms of natural causes of the evolution of species. It has been reiterated time and time again that one of the reasons for the popularity of the theory was that, as it gave biology a mechanistic theory of species change, it furnished materialists with further arguments against religion. No doubt there is a large measure of truth in this statement and since Darwin's day large bodies of Churchmen have opposed the theory for this reason. By and large the Churchmen came off worst in the arguments and counter-arguments because they were on unfamiliar grounds and because their attacks for the most part were ill-advised. It was a serious mistake to attack the theory, or indeed any scientific theory, because some people used it to bolster up a philosophical theory; because the scientific theory may be perfectly correct, but the materialistic interpretation completely wrong. With the passage of time, however, the issues have become clearer, and it is difficult to maintain that Darwinism, or its modern equivalent, is essentially irreligious, although there are still plenty of people who try to make it so. There are many Christians, including Catholics, who have no difficulty in accepting Darwinism. Hence,

¹ 1940, pp. 167-168. ² 1942, p. 104.

we should suspect that any conflict between Darwinism and religion nowadays is apparent rather than real, or is due to misunderstanding of either religion or Darwinism. Both factors have been largely ignored in the past and unfortunately they are so still, with the result that, in some instances, the conflict between religion and science over this issue has been widened. As a theory of nature, Darwinism states that species evolve in a natural way, and so Darwinian biologists avoid postulating miraculous interventions for the origins of species. Biology in this important matter is thus brought into line with science and preserves the unity which is so conspicuous a feature of science in general. Divine intervention may still occur in evolution without necessarily upsetting the laws governing the process; no one seriously contends that the miraculous cures at, say, Lourdes upset the ordinary medical laws governing the processes of healing or tissue restoration.

Natural selection, as contrasted with miraculous events in nature, merely emphasizes the harmonious workings of natural causation. The contrast of natural selection and miraculous events is a good example of the order from order principle which Schrödinger¹ finds is so characteristic of living matter. In the present state of our knowledge natural selection may seem to be a rather haphazard process but it by no means follows that it is so in fact. According to the law of uniformity we would expect it to be controlled by some law or laws.² To call natural selection a chance process is misleading because the word 'chance' here refers to a statistical process of analysis of biological results; it is not a biological word. Judging from their writings some biologists would really seem to believe that there is no 'law' behind the evolutionary process, which, for scientists, is an astounding belief to hold. The whole purpose of their working life is to unravel the laws of nature concerning living things, but in their greatest generalization by a misuse of words the impression is given, and even fostered, that there is no law. If the word 'law' here is transcribed into 'cause', or again into 'purpose', an explanation of this suicidal belief becomes evident. It is seen in Weismann's statement that biologists must believe in natural selection, otherwise a principle of design must be assumed,³ or as

¹ 1951.

² Quoted from Marquis of Salisbury's Address, 1894.

³ See page 203.

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T. H. Huxley said¹: 'It will carry us safely over many a chasm in our knowledge, and lead us to a region free from the snare of those fascinating but barren virgins, the Final Causes.' A modern writer, J. S. Huxley,² put a similar point when he wrote: '[Evolution] is just as much a product of blind forces as is the falling of a stone or the ebb and flow of the tides.'

There have always been religious people of all kinds who have believed in evolution and its various theories, including Darwinism. It is tremendously important, therefore, to realize that Darwinism is a theory of secondary causes and as such it implies the operation of the First Cause. As a harmoniously working law of nature it does not detract from our conception of the dignity of God by giving us yet another example of a natural law which seems to be chaotic in its workings but is beautiful and exact in its results. 'How incomprehensible are his judgments, and how unsearchable his ways! For who hath known the mind of the Lord? Or who hath been his counsellor.'³

One cannot discard a scientific theory merely because certain people find it amenable to materialistic and anti-religious interpretation. Surely history has shown that to oppose or condemn a scientific theory for this reason often results in an increase of scepticism regarding religion rather than the reverse. It becomes necessary for religious philosophers to counteract these tendencies by a truer approach to the scientific theory, enlarging on its inherent goodness which it must possess if it furnishes a correct natural explanation of some natural phenomenon, unless indeed it is purely neutral in its effects on human thought. A materialistic interpretation can always be countered by a theistic one.

There is another important reason why Darwinism was seized upon so avidly during the last century, and this reason also probably explains why Darwinian ideas became accepted by biologists in particular. This reason is found in the way Darwin arranged the material in his book. He began his *Origin of Species* by discussing variation and the effects of human selection on domestic breeds; then he passed to variation under nature and so to natural selection; and then he marshalled the known evidence for evolution. The psychological effect of this arrangement on Darwin's biological contemporaries must have been great because they found his theories so compelling and reasonable, and held out

¹ 1893, p. 27. ² 1942, p. 176. ³ St. Paul's Epistle to the Romans, xi: 33-34.

such hope for the future in biology that they were eagerly accepted. Darwin gave biology a unifying principle which showed promise of making biology a true and orderly science. The trust placed in his evolutionary evidence and theories has not been misplaced because, with the passage of time, the idea of evolution has developed and become further rationalized in men's minds. In some cases, however, the importance of the theory has been over-emphasized; nevertheless, biology is now a unified science, and is further strengthened by being analysable mathematically in some branches. Further, many of the biological objections or criticisms of early Darwinian theory have been satisfactorily answered, or have taken on a new meaning as knowledge of the subject advanced, or have vanished because of earlier misunderstandings of the biological nature of the facts involved. As a result, Darwinian theory has found its important place in the modern theory of organic evolution.

j. AFTER DARWIN

The *Origin of Species* is reputed to have been sold out on the very first day of publication, and since then it has gone through many editions and reprintings. Almost immediately after publication of Darwin's theory violent controversies arose. In an age when man obviously stood apart from other created things, the idea of an evolutionary scheme which might include man was a rude awakening and was inevitably bound to provoke opposition. And due to many circumstances this opposition became sadly misdirected and largely futile. In biology, evolution quickly became the master-key to many doors and because the theory was well based on sound scientific principles it was highly successful. And so both biologists and religious people were to blame for the interminable arguments and counter-arguments. Misconception was the order of the day and, under such conditions, the task of giving a true interpretation of evolutionary theory was rendered exceedingly difficult for those who contended that there is no inherent contradiction between evolutionary theory and religious belief.

Today we can look at these earlier controversies with a more chastened attitude and we can see how nearly all of it was really unnecessary and that progress in both biology and religious inter-

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pretation was greatly retarded for a generation or two. We have now a much better understanding of the relation between evolution and religion, but the effects of the Darwinian controversies still remain. These effects are seen in those biologists who cannot envisage any explanation beyond a materialistic one, and among those religionists who, discarding a modern literal historical interpretation of the Bible, have watered down its meaning until practically nothing is left, or who, realizing that evolutionary theory has been made wide use of by materialists, have attacked the biological theory itself instead of the interpretations put upon it.

Thus, after the time of Darwin, the evolutionary theory grew rapidly in content and meaning with an ever-increasing tempo until today we have in it one of the most highly developed and complicated theories that any man, or group of men, have ever produced. The strong point of the theory lies in its workability and in the universality of its appeal to biologist and non-biologist alike, to theist, atheist, agnostic and pagan also.

Many famous biologists, such as T. H. Huxley, Hooker, Romanes, Wallace and the geologist Lyell, to mention only some of the older ones, strongly supported the Darwinian theory and established it in the biological world. We must not think, however, that there were no serious objectors or objections to the theory as it was originally propounded by Darwin. Most of the informed Darwinian critics attacked a single point in the theory and relatively few wrote sustained attacks on the basic tenets of Darwinism. In the Darwinian period it is always necessary to distinguish between attacks on the evolution theory itself and those on Darwinism, or natural selection as such. Many people accepted evolution as a reasonable explanation of the known facts but they did not accept Darwin's theory of the way evolution occurred. It is beyond our purpose in this account of the growth of the evolutionary concept to give much information about these early Darwinian controversies and objections. It is sufficient to our purpose to point out that both Darwinism and the evolution theory in general were attacked from the very beginning and we may mention Mivart,¹ Jenkins² and Korschinsky.³ For fuller information the reader may consult Kellogg⁴ and Fothergill.⁵

¹ 1871.

² 1867.

³ 1889, 1901.

⁴ 1907.

⁵ 1912.

In the biological world the immediate result of the advent of Darwinism was the stimulation of research in all directions. Biologists now were not so much interested in classification for classification's sake, but they began to look for lines of descent and genetic affinities among organisms and to search for further evidence of evolution. One of the chief but later results of the theory of natural selection was that a search for the mechanism of this causal explanation of the evolutionary process was begun. Thus the period between the publication of the *Origin of Species* and the rediscovery of Mendel's principles in 1901 was a very fertile one in the history of biology. With the rediscovery of Mendelian principles the formulative period in the history of evolutionary ideas ended and the modern period began. But in the modern period the general outlook gradually became radically altered due to an increasing knowledge of the mechanism of heredity which had been nearly completely denied to biologists and natural historians prior to about 1900.

In order to complete the outline history of evolution given in this chapter it is now only necessary to indicate a few chief concepts which arose after the time of Darwin and which bear directly on the evolutionary theory and which have contributed to its modern developments. Thus, it is only necessary to mention Weismann's theories and the advent of the mutation and genetical theories.

Schleiden and Schwann had laid the foundations of the cell theory in 1838 and 1839. In 1854 Newport actually observed the process of fertilization when he saw a spermatozoon enter a frog's egg. While in 1859 Hertwig contended that of the two nuclei which fused in fertilization, one ultimately came from the male and the other from the female parent respectively. Ten years later von Kölliker, Weismann and Hertwig independently came to the conclusion that the nucleus is the actual part of the cell which bears or carries the hereditary substance. From this knowledge Weismann¹ developed his germ-plasm theory which now forms one of the basic concepts of modern cytology and genetics.

Weismann's great contribution to biology was the recognition that the *somatoplasm*, or body, is distinct from the *germ-plasm* or actual reproductive part of the body of an organism. These two parts are early differentiated in the developing fertilized egg, so

¹ 1902.

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much so that Weismann contended that the germ-plasm is continuous from generation to generation. Such a conception is fundamental and leads logically to the view that only the germ-plasm is concerned in heredity. It follows that before change or evolution can take place in an organism the germ-plasm must first of all be altered. Since Weismann's day this concept has been accepted and hence the majority of causal evolutionary investigations have centred on the ways in which possible changes in the germ-plasm may occur and the consequences of such changes. Weismann thus laid the foundations on which subsequent workers could build after the rediscovery of Mendelian principles to produce the modern theory of heredity. It should be pointed out that no matter how early the differentiation of the somatoplasm from the germ-plasm, both of these regions have a common genesis in the fertilized egg and the first few cleavage cells in all cases, at least in higher organisms.¹

Mutationism, or heterogenesis, was probably first put forward by Korschinsky in 1889, but the mutation theory is generally ascribed to de Vries who first brought forward observational and experimental evidence for it in 1901. By this time and due to the work of Bateson² it was recognized that there were at least two kinds of variations. All variations were alike to Darwin. He did not distinguish between the various kinds and he assumed that all of them were inherited. The variations which Darwin thought chiefly responsible for evolution were those ever-present small variations which were considered to produce change in the species by accumulation. Such variations were often called Darwinian variations. In 1894, however, Bateson focused the attention of biologists on these variations which are more correctly described as fluctuating variations, when it became recognized that they are exceedingly common in all species and that they seem to depend on the environment for their production. They really represent the response of an inherently plastic species to small local changes in its surroundings and they are not in fact usually inherited. Nowadays they are generally called modifications and as they are not inherited they can have no effect on the evolution of species.

However, there are variations which just arise suddenly and for this reason they used to be called saltations or sports. De Vries gave them the name *mutation* and they may also be called de

¹ See also page 153.

² 1894.

Vriesian mutations to distinguish them from other types of variations or mutations discovered later. The de Vriesian mutation is generally a large variation which is produced by some change in the germ-plasm and it is thus permanent. Hence de Vries was led to consider that it was these variations which are really concerned in evolution.

De Vries¹ worked with the Evening Primrose (*Oenothera lamarckiana*). He grew this plant in his garden for seven generations and out of a total of 54,343 plants, he found 894 definite mutations which fell into seven distinct groups. Some of these mutations were produced only once or a few times, while others appeared in each generation. The important point about them was that, once produced, they were fixed, that is, they bred true. In nature such mutations occurred in all directions, and some were adaptive and some were not. De Vries' mutation theory thus fitted in with Darwinism to the extent that natural selection was still operative. The new theory differed from the older one in choosing certain large variations as the raw material of evolutionary change. Another essential difference was that Darwinism envisaged a continuous process of evolution by means of scarcely perceptible changes, while mutationism led to discontinuous evolution.

The careful experimental work of de Vries soon led to its general acceptance by biologists and evolution by means of mutations became recognized as one of the means of evolutionary change. Later it was discovered that the plant de Vries had worked with was, in fact, a very complex hybrid and a cytogenetical interpretation could be given for the sudden but consistent production of mutations. Hence de Vries' mutations were not actually mutations in the strictly limited genetical sense, but they were cytological types. Nevertheless, other organisms produced sudden large mutations for which no cytological interpretation was given and so the theory remained.

When Mendel's work on inheritance in garden peas was rediscovered in 1901 by Correns, de Vries and Tschermak, it soon enabled biologists to construct a new mathematical theory of genetics. It is important to point out that modern genetics is concerned with a particulate theory of heredity. It deals with particles or units called *genes* or *factors* and it seeks to explain how these genes move in and out of generations of individuals. With-

¹ 1901, 1903.

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out modern genetics based on this conception of itinerant genes, evolutionary theory in general would probably have made little headway.

With the rise of modern genetics came the discovery of gene mutations produced both naturally and artificially. Soon the connection of such small mutations to evolution was recognised leading to the modern theories of evolutionary causation. As some gene mutations were found to be small, exerting extremely small effects on organisms, it was soon realized that they in fact replaced the non-inheritable Darwinian variations. Hence to a certain extent modern evolutionary theory has become a developed Darwinian theory with natural selection in a foremost position.

Consideration of these modern discoveries shows that they are quite distinct in type from those underlying earlier theories and ideas which we have outlined in this chapter and hence they are left for separate and detailed treatment in later chapters (3 and 6). Having given an outline story of the development of evolutionary ideas up to the beginning of modern times we will now concentrate on the evidence which is put forward to show that an evolutionary process actually does occur in nature (Chapters 3 and 4).

Chapter III

The Classical Evidence for the Occurrence of Organic Evolution

I. INTRODUCTION

A PHRASE which recurs in certain kinds of evolutionary literature is: 'but however pleasing such a belief might be it could not be held by *savants and enlightened people*', or some variation on that theme. In this way some evolutionists try to convey an impression to their readers at the beginning of some explanation or argument that they are right and the other fellows are wrong. No doubt this sort of thing is just a trick of the propagandist, but many people who use such phrases would be horrified at the thought of being mere advertisers for evolution. We have mentioned this unfortunate ingredient of some evolutionary literature because we are now at the beginning of the controversial part of our subject, although there is an increasing number of evolutionists who assert that the matter is now beyond argument. The evolutionist, however, is just as likely as anyone else to make mistakes and wrong judgments, or to be just plainly wrong. We can all take reassurance from Miguel de Unamuno's words¹ that 'If a man never contradicts himself, the reason must be that he virtually never says anything at all.'

Evolution, in Darwin's opinion, was a process by which all living things had descended ultimately from 'one or a few' initial progenitors. He collected together and advanced what we may now call the classical evidence for the occurrence of organic evolution. Whether he *proved* its occurrence or not is another matter, and it still logically remains so in spite of foremost evolutionists saying that the existence of evolution in this sense is 'an incontrovertible fact'.

It may be instructive to consider some other conceptions of evolution in relation to Darwin's. The following are all taken

¹ Spoken to and quoted by E. Schrödinger, 1951, p. 76.

from a symposium on evolution edited by F. Mason (1928) in which each chapter was written by a different authority. D. S. Jordan (p. 1), a chancellor of a university, wrote: 'By evolution, as the word is now used, we mean the universal process of orderly change.' In this definition the whole of the cosmos is included. J. A. Thomson (p. 13), a professor of natural history, wrote: 'Evolution means a way of becoming.' H. S. Jennings (p. 24), a professor of zoology, said: 'The doctrine of organic evolution is the doctrine that animals and plants are slowly transforming, producing new kinds; that they have done this in the past and are continuing to do it now.' Professor MacBride (p. 49), a zoologist, considered that 'According to the theory of evolution as it is applied to zoology, the fundamental likenesses of, or homologies among animals are the expression of blood relationship.' W. B. Scott (p. 81), a professor of geology, wrote: 'The theory of evolution—that all living things now in existence have arisen by natural descent, with modifications, from ancestors that might be traced back, step by step, to unknown simple forms of life.' Sir A. Smith Woodward (p. 127) considered that 'So far as it goes, all the evidence points in the same direction—to the slow and regular advance of the world of life in the way already stated. No conflicting evidence has thus far been discovered.' The editor of the symposium, F. Mason (opp. p. 110) wrote: 'The essence of evolution is unbroken sequence.'

Starting with Darwin's conception of evolution it is thus obvious that different biologists have different conceptions of the process. At one extreme we have the definition of evolution as a descent from one, or a few, original organisms; at the other extreme we see evolution as mere orderly change, or a way of becoming; and in between we learn that the essence of evolution is unbroken sequence. The only thing in common between all these conceptions of evolution is the implied statement that some kind of evolution has occurred. Hence, if we are told that evolution is a fact, and then, from this fact, very wide implications are drawn touching on the nature of man, it is important that we should first enquire about the fact. Possibly everyone would accept evolution as a process of orderly change as we see it now, but many people would not agree that all living things are descended from one original ancestor, i.e. that monophyletic evolution is a *fact* as distinct from a probability, or from a

working hypothesis. Thus, it becomes necessary to examine the reasons for belief in evolution. We wish to ascertain the limitations, if any, attached to statements about evolution. Evolution may be too far-reaching a concept to accept on faith alone. Some evolutionists may say we are being obscurantist, reactionary, uninformed and so on, but the truth is we are merely being scientific and sensible.

The evidence for evolution has been described several times. Our purpose here is not to go into too great detail but yet to give enough to enable the reader to form a balanced opinion. If the reader wishes for greater detail he must go to individual texts which deal with specialized aspects of the subject. We will consider the type of evidence presented by biologists and examine the justifications for the conclusions if this is necessary, and then give some criticisms which may have been held against the conclusions, or statements, made. In Chapters 3 and 4 we are chiefly concerned with what we have called the classical evidence; the modern genetical evidence will be given in Chapters 5 and 6.

2. EVIDENCE

Charles Darwin first assembled the various lines of evidence for the occurrence of organic evolution. In his day he knew of five lines and since then one other has been added. We will deal here with the first five of these. These lines of evidence are taken from different branches of science as follows: (a) evidence from morphology and comparative anatomy; (b) evidence from classification of plants and animals; (c) evidence from embryology and serology; (d) evidence from paleontology; (e) evidence from geographical distribution of plants and animals; (f) evidence from genetics and related subjects.

In considering evolutionary evidence, especially that from comparative anatomy, the concepts of homology and analogy are often used and they should be understood from the beginning. The English comparative anatomist Richard Owen first gave precise meaning to these terms. In 1843 he defined an *analogue* as a part, or organ, of one animal which has the same function as another part, or organ, in a different animal, and *homologue* he defined as the same organ in different animals under every variety of form and function. The difference between these two words is

thus fundamental for the one is relative to the function of a part independent of its morphology, while the other is relative to the morphology of a part independent of its particular function. A modern definition would only add to this the necessity for a study of the developmental history of the organisms concerned before arriving at a conclusion. An example of analogy is seen in the porpoise, the extinct ichthyosaur, and a fish. They are analogous in their common fish-like bodies, but the first is a mammal, the second a reptile and the third, of course, is a fish. An example of homology is seen in the thyroid gland which de Beer¹ described as showing a perfect homologous series. In the *Amphioxus* the endostyle consists of tracts of glandular tissue separated by ciliated cells which waft mucus along the structure; in the Ammocoete larva of the lamprey *Petromyzon*, a structure identical to the endostyle is found, but in the adult lamprey this endostyle loses its cavity and its ciliated cells, but the duct becomes the thyroid gland which is found in all higher Craniates. Thus the thyroid and the endostyle are strictly homologous although their functions are completely different. In some cases, however, homologies break down, as for instance among the bones of the skull of some fishes.² The principles of homology are considered to indicate the deeper relationships of animals and their parts which lead to the recognition of common descent among them, or of their ultimate genetic relationship.

(a) *Evidence from comparative anatomy*

Owen first recognized an archetype in animals which was a hypothetical type of generalized structure potentially embodying all organisms in a group. An examination of animals and plants shows that there are large groups called *phyla* in each of which there is a common plan of construction. This plan covers the major parts and appendages of the body and often extends down to detailed structures. Each phylum is distinct, although some of them may be analogous in form as in various types of worms which have a worm-like outward shape but are completely different in their morphology and structure. Older classifications generally gave about ten or twelve phyla in the animal kingdom, but modern authorities recognize about twenty of them. The more important ones are as follows: (1) *Protozoa* (unicellular and

¹ 1941, p. 477. ² Westoll, 1936.

colonial forms), (2) *Porifera* (sponges), (3) *Coelenterata* (hydroids, corals, and jelly-fishes), (4) *Graptolithina* (extinct and doubtful), (5) *Platyhelminthes* (flatworms), (6) *Nemertinea* (hair worms), (7) *Nemathelminthes* (thread worms, nematodes), (8) *Trochelminthes* (wheel animalcules), (9) *annelida* (segmented worm), (10) *Bryozoa* (sea-mosses), (11) *Brachiopoda* (lampshells), (12) *Echinodermata* (sea-urchins, starfishes), (13) *Mollusca* (molluscs), (14) *Arthropoda* (arthropods), (15) *Chordata* (vertebrates).

The number of phyla among plants is very much less; they are: (1) *Algae* (seaweeds, etc.), (2) *Fungi* (chlorophyll-less plants), (3) *Bryophyta* (mosses and liverworts), (4) *Pteridophyta* (ferns and fern allies), (5) *Spermatophyta* (seed plants, flowering plants and conifers). Plants show a special order called *Lichenales*, or lichens, which consist essentially of an alga and a fungus living together in very intimate association (symbiosis).

The members of each phylum, although built on a common plan, are generally considerably modified, so that each phylum may contain a large number of different types of organisms. Some further details are given below to illustrate what is meant by a plan of construction and by variation within the phylum.

1. *Protista*. These organisms comprise a miscellaneous group, but all of them are unicellular and have no tissues as such. Most of them live in water, but some are parasitic. Examples are *Amaba*, *Paramecium* and the malarial parasite.

2. *Coelenterata*. Most of these are marine and they are all aquatic organisms, but the group is very varied. They are all radially symmetrical and possess a hollow body, the cavity of which functions both for digestion and for circulation. Many of them have tentacles and stinging cells. Common examples are *Hydra*, sea anemones, jelly-fishes and corals.

3. *annelida*. These comprise the jointed or segmented worms familiar to us as the ordinary earthworm. They are characterized by possessing a segmented body, a closed blood system, a well-developed body cavity, or coelom, and a double ventral nerve cord. They have no jointed appendages. Other examples are seen in the marine worms and leeches.

4. *Arthropoda*. In a number of individuals this phylum probably outweighs all the rest because it includes such diverse forms as the millipedes, centipedes, crustaceans, insects, scorpions, spiders, crabs, shrimps, barnacles and mites, forming about three-

quarters of the number of all animals. Their basic plan of construction is very characteristic. They are bilaterally symmetrical, segmented, and have an open blood system, a small coelom, a double ventral nerve cord, a thick cuticle which often forms a hard exoskeleton of chitinous substance, and they have jointed legs and other appendages, which are not possessed by all, such as wings, antennae and spinnerets.

5. *Chordata*. This phylum is commonly called the *Vertebrata*. It is a large group comprising all the higher animals such as fishes, frogs, birds and mammals. The distinctive characteristics are bilateral symmetry with a perforated pharynx, a hollow dorsally-situated nerve cord and an axial notochord which is generally replaced by a vertebral column. There is an internal skeleton of bone or cartilage and usually a well-developed heart, brain and limbs.

Among plant phyla we may notice the following:

1. *Fungi*. These plants are exemplified by the common mushrooms and the ubiquitous moulds. They lack chlorophyll and hence they cannot synthesize the basic carbohydrates necessary for their metabolism. Thus their mode of nutrition is said to be heterotrophic, and they live either as saprophytes on dead organic matter, or as parasites on living organisms, or as both. Their plant body is called a *thallus*, that is, it does not have root, stem or leaf. Some of them are unicellular and aquatic, and others are multicellular but they never form complicated tissues like those found in the higher plants. The fungi for the most part form a very sharply-delimited group.

2. *Pteridophyta*. This phylum includes a variety of plants such as the ferns, horsetails and club-mosses. They all possess stems and leaves which may be reduced or absent in special cases, a vascular system and distinct sexual and asexual generations which normally alternate. They do not form seeds.

3. *Spermatophyta*. These comprise all those plants which produce seeds. Examples are the ordinary flowering plants and conifers. They possess root, stem and leaves which may be modified, a complicated vascular system, flowers of different kinds; the sexual generation is reduced and never forms a separate plant.

On first hearing it said it may sound rather surprising to be told that a fish, such as a shark or a dogfish, has the same common

ground plan as a man, or other mammal. They look so different; they are so different in many ways; their conditions of life are so completely different and yet they are both Chordates because of the fundamental resemblances between them. In the early foetal stages of both they agree in their digestive, respiratory, reproductive and circulatory systems. They have the same chief divisions of the body; the same segmentation of the vertebral column, the same composition of the skull; the spinal cord and the brain all have a similar basic ground plan. Fishes like the shark were in existence in the Devonian Period millions of years before the advent of man. These fishes, however, have changed relatively little since these ancient times, whereas man has reached the highest stage in evolution, but he still remains a Chordate animal.

About 1846 Owen, Geoffrey St. Hilaire and others commented on homology of structure in animals. Darwin, in successive editions of *The Origin of Species*, devoted some considerable space to this topic and noted that homologous organs were easier seen in the higher vertebrates than in the lower ones because in the latter there are not so many indefinite repetitions of parts. Later, in 1897, Romanes devoted a whole chapter to the consideration of homologies and gave many examples. Because these examples are so illustrative many subsequent writers have made use of them. The essential feature of homologous organs, while retaining a common basic structure, is the occurrence of modifications to suit different functions. One of the best examples is seen in the pentadactyl limbs of higher vertebrates such as whales, seals, porpoises, bats, birds, reptiles, frogs and man. In all of these the same five-sectional plan of the limbs is seen but it is modified variously as swimming, flying or grasping organs. In the whale indeed the bones are embedded in the blubber and are considerably reduced, but still the series is complete. In these animals the modifications are brought about by alterations in the proportions and relative sizes of the individual bones making up the limbs, or even by the disappearance of certain bones. A beautiful example of such reduction is shown in the feet of the hippopotamus, pig, deer and the camel (Figure 1). In the hippopotamus the first digit is represented only by a small bone, while the second and fifth digits are jointed but are decidedly smaller than the third and fourth digits. In the remaining members of the series, a



Fig. 1. Fore bones of four different forms of the actinodactyl type, showing reduction of the number of digits coupled with a greater consolidation of the bones above the digits. Reading from right to left, hippocampus, pig, deer and camel. (From Romanez, 1895.)

progressive reduction is seen in the size of the second and fifth digits, until they finally disappear in the camel and only the third and fourth digits are left.

In the skulls of all vertebrates corresponding bones are found which become fused together and they are considered to be modified vertebrae. The lungs of higher vertebrates are homologous with the air bladder of higher fish. Both organs may be derived from the paired lungs of some primitive Dipnoid fish. Other examples of homologous organs are seen in (a) the appendages of crustaceans, (b) the mouth parts of insects, (c) the teeth of mammals, and (d), as we have already noted, the endostyle of *Amphioxus* is homologous with the thyroid gland of higher types.

Turning now to plants, an interesting homologous series may be seen. To begin with, a structure called an archegonium is first found in liverworts and mosses. It is the female reproductive organ and produces the female gamete, or egg, called an oosphere. The archegonium consists essentially of a swollen basal part containing the egg and surrounded by a wall of two layers of cells, and a long neck. When mature the cells in the interior of the neck become mucilaginous and the apex becomes open. A clear passage is thus provided for the male gamete, or sex cell, to reach the egg. Such an archegonium is also found in ferns and gymnosperms (conifers). It is thus common to several phyla. The archegonium is, of course, considerably modified throughout these groups.

The life histories of plants show further homologies as between phylum and phylum. In the Bryophyta (mosses and liverworts), the plant is the sexual generation, or gametophyte, and bears the sex organs comprising the female archegonium and the male antheridium. When fertilization occurs the female egg unites with the male antherzoid to form a zygote, or oospore, as the product is called. From the oospore the new generation, or sporophyte, develops. But this generation never becomes completely separated or independent of the gametophyte. The sporophyte is partially dependent on the gametophyte. Eventually it produces asexual spores in a capsule and when these are liberated they germinate to form a filamentous structure from which the new gametophyte is budded off. There is thus a distinct alternation of generations in which the sexual gametophyte is the plant itself and the asexual sporophyte is carried on it. In the Pteridophyta (ferns and fern

allies), however, the position is reversed. The pteridophytic plant is the sporophyte and it produces asexual spores inside a sac-like body, or sporangium. The sporangia are borne on the leaves, or in other ways, and from a spore a new gametophyte arises again. In some pteridophytes, such as the horsetails, there are separate male and female gametophytes; in others the gametophyte has been drastically reduced—for instance in *Selaginella* the female gametophyte is contained within a large megasporangium. It is multicellular and produces archegonia resembling those of the bryophytes but they are smaller and the basal part is sunken. In *Selaginella* the male prothallus (gametophyte) consists only of a single prothallial cell while the remainder of the structure forms the male antheridium. Thus in the Pteridophyta not only has the relative importance of the gametophyte compared with the sporophyte decreased, but throughout this group there is a further decrease until the male gametophyte is represented by only a single cell. In the gymnosperms (cone-bearing plants) there are two prothallial cells contained in the pollen grain, while the female prothallus forms part of an ovule. In the flowering plants the reduction has been completed for there is no true female prothallus in the ovule, but the male prothallus is still represented by a single prothallial cell. Thus it can be said that an alternation of generations is shown by all plants from liverworts to flowering plants.

Finally, a very characteristic homologous series is seen in the lower fungi. Here, among a group of the filamentous fungi called the Mucorales, asexual reproduction occurs by means of sporangiospores which are formed *inside* a sac-like wall or sporangium. The 'typical' sporangium contains many spores, but the number produced in different genera becomes reduced so that in *Chaetosporium*, for instance, the sporangium has a two-layered wall and one of these becomes the actual wall of the sporangium while the other becomes the wall of the spore. In *Blakeslea* and *Cheiromyces* the sporangium has only a single layer which is also the outer layer of the spore. The spore has thus become a conidium. Such a conidium, however, differs from ordinary conidia in being indehiscent—normally conidia are spores produced *externally* at the end of a stalk which fall off, or are shot off violently. A similar change from the typical sporangium with contained spores to a single externally formed conidium is seen also in the

Peronosporales and Entomophthorales which are other groups of these fungi. Hence the conidium and the sporangium are considered to be homologous.

Homology is an indication of divergence from a common type and it bears a close relationship to function—the modification of the pentadactyl limb into legs, paddles, etc., illustrates this point well. On the other hand analogy is an indication of convergence in which completely different types of animals with basically different plans of construction have come to look alike in some respect because of the similar function which they, or the parts concerned, perform. Convergence may also be an illustration of a type of parallel evolution. We will give a few examples to show the meaning of analogical convergence. A simple example is that of the wings of insects and of birds which enable the animals to fly efficiently but which are built up on a completely different plan of construction. Again, vertebrates have walking legs which are jointed. The crustaceans, insects and spiders also have jointed walking legs which look similar in some respects but which are completely different. In the vertebrates the skeleton is inside the leg and the muscles which move them are outside the skeleton, while in the crustacea the skeleton is outside the leg, but the muscles are inside the skeleton. The whale in many respects looks like a fish. The armoured ostracoderm fishes closely resembled the Silurian *Bunodes*, a scorpion; while the outward forms of the shark (fish), a porpoise (mammal) and *Ichthyosaurus* (an extinct reptile), already mentioned, were much alike. Worms also show many different analogies; for example, some amphibians (the *Cocilkidae*), some snakes (Typhlopidae) and some lizards (Amphisbaenidae) are so worm-like that they are able to burrow underground like earthworms. Again, the *Urodele*, some *Cetacei* and *Ichthyosaurus* possess median dorsal fins like those of a fish, but structurally, of course, they are totally different. The eye of the octopus is superficially like the eye of a fish.

H. F. Osborn¹ considered that analogies of the type just mentioned show a law of convergence, or of parallelism, in adaptation. He defined this as: "The production of externally similar forms in adaptation to similar external natural forces." The necessity for adaptations may have arisen through a series of mechanical problems created by gravity, resistance of water or

¹ 1923, p. 135.

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air, or lifting movements, etc. Convergence shows that nature solves such mechanical problems by using common principles. Convergence also represents, as Osborn contended, the resultant between the mechanical problems of the environment of an organism and its physicochemical laws of action, reaction and interaction. The law of divergence as expressed by homology of diverse functional units stands in contrast to convergence, but Osborn combined both principles in one *law of adaptive radiation*. This law expresses the mode of adaptation or form of convergence and divergence. A summary of this law adapted from Osborn¹ is given below.

Table I. *Law of adaptive radiation in the external body form (after Osborn, 1925)*

1. *Divergent adaptation* by which the members of a primitive stock tend to develop differences of form while radiating into a number of habitat zones.
2. *Convergent adaptation, parallel or bioplastic*, whereby animals from different habitats enter a similar habitat and acquire many superficial similarities of form.
3. *Direct adaptation*, for example in primary migration through an ascending series of habitats, aquatic to terrestrial, etc.
4. *Reversed adaptation*, where secondary migration takes a reverse or descending direction from aerial to arboreal, arboreal to terrestrial, from terrestrial to aquatic.
5. *Alternate adaptation*, where the animal departs from an original habitat and primary phase of adaptation into a secondary phase, and then returns from the secondary phase into a repetition of the primary phase by returning to the primary habitat.
6. *Change of adaptation (function)*, by which an organ serving a certain function in one zone is not lost but takes up an entirely new function in a new zone.
7. *Symbiotic adaptation*, where vertebrate forms exhibit reciprocal or interlocking adaptations with the evolution of other vertebrates or invertebrates.

Osborn later developed the law of adaptive radiation until he was able to formulate it more completely in his theory of *aristogenesis* or biomechanical evolution. This theory will be mentioned later but for a full account the reader is referred to Fothergill²

¹ 1925, p. 158. ² 1932.

where all references are given. At this stage the importance of the law is that it exemplifies the use of morphological principles applied dynamically to evolution which clarifies the evidence for evolution. Adaptive radiation is an accepted principle of evolution and all the larger groups, especially of the higher vertebrates, illustrate it very well. Some examples of the principle will be given later under the palaeontological evidence. A serious disadvantage of adaptive radiation, however, is seen in the extinction of some highly specialized groups of animals such as the giant dinosaurs. In cases of this kind what happens is that in response to the increasing demands of the environment radiation leads to the reduction and loss, or to the over-development, of too many characteristics of an organism. If they are lost they cannot be regained, according to Geoffrey St. Hilaire's law of compensation. Thus a highly specialized animal becomes too perfectly adapted to a specialized environment and so eventually becomes extinct. De Beer¹ maintained that one of the secrets of man's evolutionary success is that he is structurally generalized, not specialized. Thus he is able to live in almost all kinds of circumstances; his mode of life is not thereby restricted.

Evolution of teeth

We cannot in this book consider the evolution of even the important morphological and anatomical systems, but it is appropriate to study one system in some detail which will show some of the methods of comparative morphology and anatomy, and the type of evidence in this section which is advanced in favour of evolution. Hence we will consider the phylogenetic development of teeth and for descriptive purposes we will consider that an evolution of teeth has in fact occurred. Teeth have been chosen as a type system because they are so important in evolutionary determinations. The material of this description is largely based on a general account of teeth given by H. V. Neal and H. W. Rand.²

True vertebrate teeth begin with the sharks, where they are seen as placoid scales. Placoid scales consist in the main of a hollow cone of dentine with a layer of enamel on the outside and a hollow pulp cavity in the centre. Such a structure develops below the surface of the body but emerges later on during the course of

¹ 1941, p. 484.

² 1939, Chap. 5.

development. In dog-fishes and sharks such scales are found all over the body, making it very tough and rasp-like. In the jaws of elasmobranch fishes there are a large number, up to about a hundred, and in the floor tissue between the jaws there are more, of these placoid scales, which have become enlarged to form true biting or holding teeth. The teeth between the jaws are quite free of the jaws and they are skin structures only. In teleost fish an advance is seen where the base of the teeth has become joined to the bones of the jaw and the number is less. In amphibia the number of teeth occur only in the two jaws and we meet with two forms of dentition—*pleurodont* and *acrodont*. In *pleurodont* dentition the teeth grow out from a ledge on the inner side of the jaw, while in *acrodont* dentition they grow on the bone of the jaw. In fossil reptiles and in crocodiles a third, or *thecodont*, condition is met with in which each tooth is fixed in a separate socket. This is the condition found also in mammals.

In the above groups of animals (except mammals) the teeth are all alike, that is, they have *homodont* dentition. In some lizards, however, they become *heterodont*, that is, differentiated into incisors, canines and molars. The incisors are cutting teeth, the canines act as penetrating teeth, while the molars are grinding teeth. Snakes have developed specially modified poison fangs. These teeth are hinged; normally they are held down and are only elevated when the snake bites.

Thus in the evolution of teeth two types appeared, first the simple conical tooth and then the compound tooth such as a molar. Compound teeth are considered to have evolved from simple teeth by a process of differentiation as follows. The simple tooth has only one crown or cone. The first stage in differentiation was seen in *Dromatherium*, a Triassic mammal, in each tooth of the upper jaw of which there was a central crown or *protocone*, with a second crown, the *paracone*, in front and a third, the *metacone*, behind. Thus these three cones or cusps were arranged in a single row. At the base of these cones there was a rim, or *cingulum*. The corresponding parts of the teeth of the lower jaw are called *proto-*, *para-* and *meta-conid*. Normally the second and third tubercles are much smaller than the primary *protocone*, but there was a tendency for them to become as large, or nearly as large, as the *protocone*. This type of tooth is said to be *triconodont*. The next stage was seen in a form such as

Spalacotherium or *Amphitherium* where the three cones were placed triangularly in relation to each other. This triangle is called a *trigon*. In the upper jaw the triangulation was brought about by the two secondary cones moving inwards, while in the lower jaw they moved outwards. The teeth are then said to be *tribuberosular*, and this arrangement ensures that when upper and lower jaws are closed the cones overlap and interlock (see Figure 1). The next stage in the evolution of these structures is seen in mammals when a talon, or posterior projection, and a fourth tubercle, the *hypacone* in the upper jaw and *hypoconeid* in the lower jaw, developed. Finally, in modern mammals, six cusps or cones have also developed. In some higher animals the cusps are separate, while in others they are joined by ridges, and in others again they are flayed out. Mammalian teeth also possess a covering called cement which may not, however, be completely round the tooth; mammalian molars also possess roots. In the mammals generally, teeth vary considerably both as to number and relationship of the different kinds and types. In some mammals absent teeth are replaced, while in others they are not. In man there are thirty-two teeth made up of eight incisors, four canines, eight premolars and twelve molars. The dental formula then is $i^2_2, c^1_1, pm^4_2, m^3_3$; see Figure 2 for illustrations of these teeth.

Vestigial organs

In organisms it is clear that some organs, such as the heart, are vital to the creature if it is to live; others, such as a limb, are necessary but not vital, while still others are said to be useless. It is this latter type of organ which we wish to consider now. The presence of greatly reduced organs in plants and animals when other organisms show similar and homologous functional structures is usually taken to mean that the reduced organs are in course of disappearance, and this view is greatly strengthened if these organs are entirely useless to the organism possessing them. Such organs are said to be *vestigial*. There are said to be numerous examples of vestigial organs throughout the higher animals, and they are found also in some plants.

In the early days of Darwinism when the search for evolutionary evidence was intense many of these useless organs were described, but the list of them is rather limited today. For example, many years ago a biologist enumerated about one hundred and eighty

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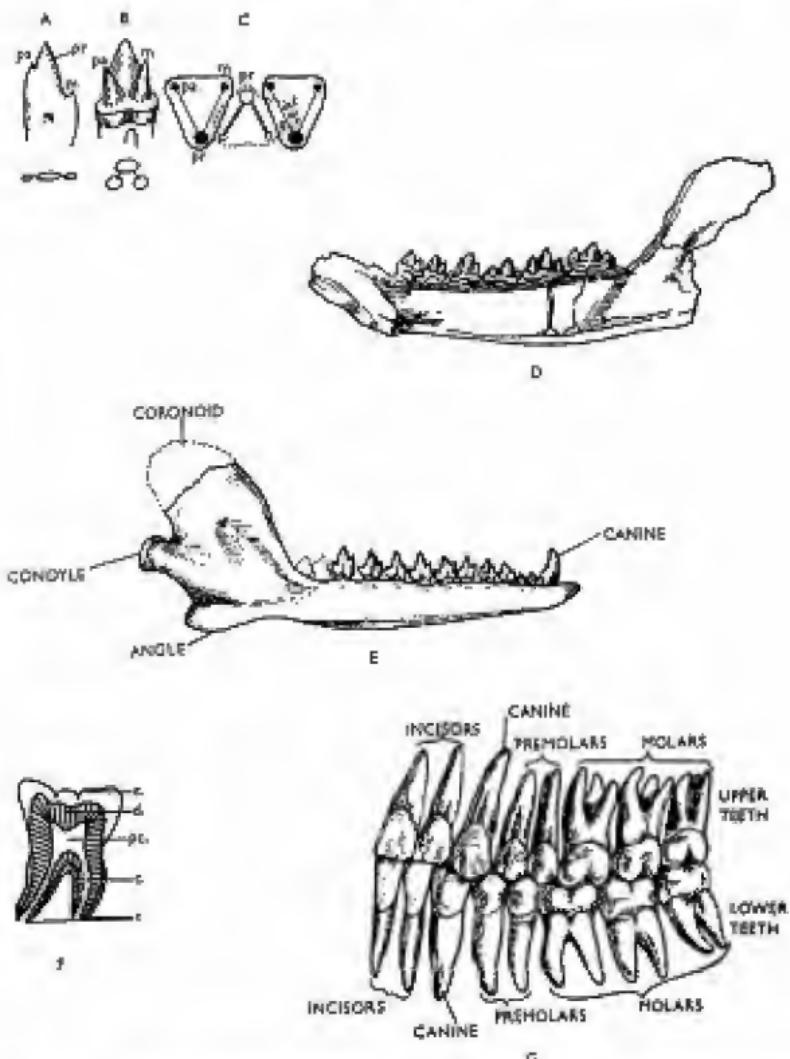


Fig. 2. Types of mammalian teeth. A, triconodont tooth of *Dimetrodon*; B, tritubercular tooth of *Sphenacodon*; C, interlocking of upper (dark) and lower (light) tritubercular teeth; D, triconodont teeth in jaw of *Tritylodon*; E, tritubercular teeth in jaw of *Diplocaelus*; F, longitudinal section of a human molar tooth; G, human teeth from the left side (formula: I₃, C₁, PM₂, M₃); m = metacone (metaconid), p = paracone (paraconid), pr = protocone (protoconid), t = talon, c = cement, d = dentine, e = enamel, p_r = pulp, r = roots. (A, B, C, G after Neal and Rand, 1939; after Kingsley, 1912; D and E from Lull, 1914; F after de Beer, 1941.)

vestigial organs in man alone; that list is now reduced to perhaps twenty or thirty. One of the difficulties involved in deciding whether or not an organ is useless lies in the fact that while an organ may be reduced in size it may still perform a useful function, and while it performs that function there may be no need for it to develop any further. Some examples of vestigial organs are given below.

At the end of the vertebral column in man there is a small group of bones forming the coccyx. This structure is said to represent the vestiges of a mammalian tail. Occasionally the coccyx seems to develop and produce a structure resembling a small and stumpy external tail (see Plate 1). Again, in the angle between the eye and the nose in man there is a fold or ridge of tissue called the *plica semilunaris*. It is considered to be the vestige of a third eye-lid or inctitating membrane found in some other animals.

A whole group of insects lacks wings, and in the case of some insects which inhabit oceanic islands the wings may be reduced to stumps. Again, sometimes one sex in insects lacks wings while the opposite sex possesses them. *Drosophila melanogaster*, that tool of the geneticist, sometimes produces wingless, or nearly wingless, forms in the laboratory. Lack of wings, or the presence of mere stumps (hapteres) represents a vestigial condition in the insects concerned which have descended from winged forms. The New Zealand *Kiwi*, or wingless bird, which is becoming extinct, has no wings but it possesses a much reduced remnant of a pentadactyl wing on each side of the body. Other New Zealand birds show a similar condition. There are several extinct wingless birds such as the Mauritian Dodo. In extinct *Moa*, this reduction was taken a stage further for they did not even possess any vestiges of wing bones.

There is no need to describe any more of these vestigial structures but a short list of some other examples will show the range of organs affected and of organisms in which they are found. The list is as follows: in female birds the right ovary and oviduct have become vestigial; many animals living in dark caves have ill-developed sightless eyes; the splint bones of the horse represent reduced second and fourth digits; the peculiar pelvic girdle and sunken bones in the whale represent reduced functionless hind limbs and pelvis. The remains of hind limbs in some snakes such

as the *Anaconda* or python, teeth that appear in the embryos of toothless whales which are never cut and are ultimately absorbed, the muscles of the human external ear, the human appendix, the lanugo or hair on the human embryo, Darwin's point on the internal margin of the human ear, additional mammae in females, shells in some slugs, and also teeth in the young duck-billed Platypus which are completely formed but are never cut through the gum, are all examples of vestigial organs. Vestigial structures are also encountered in plants in cases where the leaves are much reduced as in horsetails, cacti, *Pitcairnia*, Butcher's Broom, and stamens as in *Scrophularia*.

The anatomical characteristics of an organism are determined by the tissues composing it, and these by the cells which compose them. Ultimately the nature of the cell is determined by its chemical composition and activities. It is not surprising, therefore, that biochemistry may provide evolutionary evidence. The study of biochemical evolution is fairly new and probably in the course of time a large amount of valuable material will be forthcoming. For a good general review on the subject the reader may be referred to a book by Marcel Florkin.¹

Organisms also possess biochemical homologues and analogues. Chemicals are said to be homologous when they have a common chemical lineage, and they are analogous when they are chemically different but perform a similar chemical or physiological function. There may be degrees of chemical homology. We will give an example of each, and these examples are further valuable because the same substances are involved.

Haemoglobin is the red blood pigment found in all vertebrates. This substance is formed by the union of four molecules containing iron which are called protohaeme molecules with a protein called globin. The protohaeme molecules are identical in all haemoglobins; it is the globin part which varies in different vertebrates giving specific characteristics to the different haemoglobins. These haemoglobins are not chemically identical but they are homologous because of their common chemical lineage.

The importance of oxygen to living things is well known and it is a fact that in animals so far apart in classification as echinoderms, worms, crustaceans, molluscs and vertebrates, the transfer of oxygen from the surrounding medium, whether it is water or air,

is accomplished by certain molecules or oxygen carriers, which absorb and loosely combine with the gas from the water or air, and later give it up to the tissues as the blood circulates in the body. At the same time the waste carbon dioxide is given up to the blood. This process of exchange or transfer of gases is initiated by pressure alterations in the tissues. There are four types of these oxygen carriers in the organisms mentioned above. These are: (a) haemoglobins, with two kinds, true red haemoglobin of vertebrates and red crythrocyruorins found in invertebrates. Both contain iron and are derived from protohaeme molecules. (b) Chlorocruorins which are found in some annelids. They are the green blood pigments containing iron and are derived from chlorocruorohaeme. (c) Haemocyanins, which are the blue blood pigments found in many molluscs and crustaceans. They contain copper but are not derivatives of protohaeme. (d) Haemerythrins, which are found in the coelom (body cavity) of unsegmented marine worms (the *Sipunculidae*) forming a red-violet pigment. They contain iron but are not derivatives of protohaeme. These chemicals are completely different but they perform a like function as oxygen carriers and thus they are analogous.

We have now given some of the facts from comparative anatomy and morphology which are advanced as evidence for evolution. As homology is such a prominent concept in comparative anatomy the position of the evolutionist is clear because he contends that (a) these homologous likenesses shown so well in so many examples among all the phyla, and (b) the common plans running through each phylum in spite of the manifold diversities of form and function of the animals or organs concerned, mean only one thing and that is that a blood relationship exists between them. If we consider the vertebrate skeleton, the blood system and the nervous system alone which are common throughout all vertebrates in their basic features, a natural explanation of this fact would seem to be difficult except on the basis of descent with modifications, and this means descent ultimately from a common ancestor. The mass of evidence for this conclusion is very great indeed but it is a purely empirical conclusion. If once this conclusion is allowed then comparative anatomy and morphology become a reasoned branch of science able to investigate problems inherent in and due to the great complexities of the subjects and

their environments. Without this basic assumption comparative anatomy becomes just a long list of bare facts with little fundamental meaning except for the individual organists concerned. Indeed comparison is valueless unless some fact emerges which is further explanatory, and, in comparative anatomy, comparisons made on an evolutionary basis are very fruitful indeed. D. M. S. Watson¹ in the Silliman Lectures affirmed that the only evidence the palaeontologist can have of relationship is derived from similarity of structures, and the assumption of relationship due to similarity of structure is true enough to enable morphologists to make predictions which have been verified later.

The human mind naturally tends to make comparisons and strives to find explanations for things. *A priori*, we expect an explanation to be possible. Before the time of Linnaeus natural history looked as though it would exhaust itself due to the multiplicity of descriptions of things which had accumulated. By his classification based on likenesses Linnaeus restored order and opened up new approaches. These led the way for the comparative anatomist who, in his turn, by assuming genetic descent forced upon him by his observations, opened up further new fields of investigation and gave rise to greater generalizations. Without the evolutionary series shown by comparative anatomy no man could carry the facts of biology in his mind. The evolutionary series exhibited among the various phyla, classes and so on summarize the facts of anatomy and morphology and give a satisfying reason for the resemblances and differences between organisms. An evolutionary series is nearly always in the same direction, that is it proceeds from simpler to more complex forms, and often this progression can be correlated with changes in the environment. Osborn's law of adaptive radiation is very comprehensive and yet it merely integrates the facts as he saw them from a dynamic or energetic point of view. The full influence of adaptive radiation, however, is not seen from the comparative anatomy of living forms alone; it becomes truly significant when fossil series are also considered. For this reason we will come back to this topic later when examples will also be given. It is just as well to note, however, that Cuvier, who was the first great comparative anatomist, did not consider that his studies led to the conclusion of genetic affinity, even though he discovered the key

¹ 1911, Chap. 1.

which laid the foundations of comparative anatomy. He discovered that every part of any animal, and in some, the very smallest part, constitutes a certain index of the character in all respects of the rest, and that each part of an animal is made to fit in with all the other parts.¹ Again, Owen, the rationalizer of the ideas of homology and analogy, was led to conceive his archetypes through comparative anatomy, but he did not accept evolution until he had studied the geological history of the evolution of the horse.²

The so-called vestigial organs are undoubtedly very fascinating from a morphological standpoint. Huxley³ refers to them as 'the evidence of the useless'. It is true that, granted evolution, then their presence is easily explained as being organs which are disappearing. This interpretation, however, may lead to far-reaching conclusions, such as the derivation of the whale from land vertebrates indicated by the hidden leg bones in the blubber and the reduced front paddles. Whatever their true significance, they do show that great changes may occur in various organs. Most evolutionists who write about vestigial organs seem to assert that only an evolutionary explanation can account for them. It is unsafe to be so dogmatic, because the evolutionary explanation may be only one of several possible explanations. These organs could just as well be organs which are beginning to develop or evolve as organs which are degenerating to extinction.

In fact D. Dewar⁴ found that practically all of the organs described as useless were functional. He denied that they really supplied evidence for evolution but rather supported special creationism. He asked, if organisms are full of vestiges, as some people assert, why are they not also full of nascent organs as he contended they should be on the evolutionary theory? Dewar argued this point in detail very convincingly with H. S. Shelton.⁵

There are many unsolved problems in comparative anatomy which evolutionists would like to see settled. The most important of these concern the relationships between the phyla. In plants, as already shown, the archegonium is common to several phyla, but this is only one of the few connecting links between them and by itself it is by no means indicative of a common descent of the phyla. Again, the fungi and the algae are two quite unrelated

¹ See Fothergill, 1952, 88 *et seq.*

² 1914, p. 63.

³ See Fothergill, 1952, pp. 92-97.

⁴ Various works, 1931, 1934, 1940.

⁵ 1947.

groups. In the past it was assumed that the fungi had evolved from the algae by loss of chlorophyll and degeneration. This assumption itself for such a large ubiquitous and varied group as the fungi was scarcely scientific, because the rule, if rule there be, is for evolution to be progressive not retrogressive except in special cases which certainly do not concern phyla or other large groups. The derivation of the fungi from the algae was not an *a priori* expectation. The idea still persists in many modern textbooks, but the only evidence for it is the occurrence of some reproductive structures in a few algae which superficially resemble similar structures in some fungi. Here we have an example of comparative morphology gone mad, and perhaps the reason for its onetime general acceptance was a conviction that the fungi *must* be derived from the algae because the latter *must* have been the first plants.

At a meeting of the Linnean Society discussing the classification of the fungi, B. Barnes¹ said: 'It does not seem necessary to question the prevailing views that the phycomycetes include the simplest known fungi, but there is no reason to think that they have algal affinities.' While at the same meeting J. Ramsbottom¹ remarked: 'When fungi had more scant treatment at the Universities even than at present, they were regarded as decadent algae and superficial similarities were listed to show from whence they originated.'

One of the great problems among vertebrates concerns their ancestry. The vitalist Hans Driesch² as long ago as 1908 found that vertebrates had been 'proved' to be descended from firstly amphibians, secondly annelids, thirdly *Sagitta* worms, fourthly spiders, fifthly *Limulus*, and sixthly echinoderm larvae. Modern writers can now take a more open view of the matter; for example, H. V. Neal and H. W. Rand³ wrote: 'The shift of morphological opinion has led to increased tolerance of the view that the larger subdivisions of the animal kingdom have made their appearance independently and much earlier in the history of organisms than morphologists formerly supposed.'

The geneticist T. Dobzhansky, when discussing the question of the manifold effects of genes (pleiotropy) in which he showed that the obvious effect of a gene was not necessarily the most

¹ 1954, p. 3 and p. 9 respectively. ² 1908, p. 256.
³ 1939, pp. 427-8.

important effect it had on the organism, summed up the main points of the question of vestigial organs and gave the geneticist's viewpoint. He wrote:

However, a complete disappearance of these useless organs, both in the adults and in the embryos, would necessitate radical changes in the basic embryonic processes of organ formation and differentiation. The coccyx is a part of the axial skeleton, and the gill bars arise in the process of formation of the head and the neck. The problem should, therefore, be turned around, and it may be asked what advantages would accrue to the organism from such radical alterations of its development. The development is more than summation of 'unit characters' or unit processes. As emphasized especially by Schmalhausen,¹ development is a highly integrated process, and progressive evolution from the lower to the higher organisms has on the whole tended to make the integrations more and more thorough, and to make the basic developmental processes more and more autonomous from direct stimuli emanating from the environment.²

(b) *Evidence from plant and animal classification*

This line of evidence is related to comparative anatomy and morphology in its gross effects, although one must not confuse an anatomist with a systematist. Their work and their approach to biology is quite different. In a sense it may be said that one is analytic and the other synthetic in their methods. In an earlier chapter we mentioned the part classification played in leading to a formulation and development of the concept of evolution, and there is no need to repeat the information given. It is an amazing feature, however, that since the very earliest times people have tried to classify things, not only living organisms but practically everything else. Our minds seem to boggle at the multiplicity of objects around us and strive to reduce their number in order to make them comprehensible. By doing this we seem to gain a new insight into the relationships of things. For instance, many organisms grow together in a field; some may be useful, some may be weeds, but when we consider them as a whole, that is, as a population, new ideas may spring to our mind which were not so evident when we looked at them as individuals in the population. So it has been said that the aim of the biologist is to classify all

¹ 1949. ² Dobzhansky, 1956, p. 337.



1. Photograph of a Tamil boy, 11 years old, showing one form of external tail. (From Osman Hill, 1954)



Normal



Globe



Pineapple



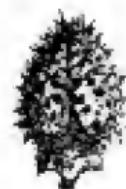
Cocktail



Flax



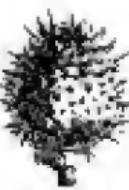
Flax



Puffed



Refined



Butting



Gloomy



Microscopic



Elongate



Spinach

2. Capsules of the 12 primary trisomics ($2x + 1$ types) of *Datura stramonium* with a capsule of a normal ($2x$) plant above. (From Blakeslee, 1930)

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living things, implying that when this is done his tasks will be finished. Like all aphorisms this one, too, is an exaggeration, but there is a good deal of truth in it.

Hence from early times naturalists have classified, using at first quite arbitrary criteria of classification such as useful or not useful, or into trees, shrubs and herbs. With the use of better criteria the subject became rationalized. Species is one of those 'transcendental' words which it is very difficult to define and there is really no need to do so at this stage except to mention that previously a species was looked upon as an individual type of, say, a buttercup, but nowadays it is regarded rather as a population of closely related types of buttercups. This loose definition is not meant to be exact; it is merely a starting point, and the implication is that there is such a thing as a species at least in our abstractions from nature. After all biology itself is one huge abstraction. Examination, of course, shows that species vary, that is, there are varieties. Observation also shows that there are different kinds or species of buttercups which are not merely varieties but are something in a higher category. That is, species fall into a genus. Then we have plants such as anemones which resemble buttercups in some respects yet show distinct differences. The anemones form another genus, and in this way we are led on to families, orders, sub-classes, classes, sub-phyla, phyla and kingdom. The ordinary buttercup is thus classified as follows; the capital letter or abbreviation after the species name gives the name of the person who first named the organism:

variety:	<i>pumilus</i> Wahl.
species:	<i>acris</i> L.
genus:	<i>Ranunculus</i>
family:	Ranunculaceae
order:	Ranales
sub-class:	Archichlamydeae
class 1:	Dicotyledonae
sub-phylum:	Angiospermae
phylum:	Spermatophyta
kingdom:	Plants.

All these kinds of classifications vary according to the criteria used by the writer and the importance he gives to the various

categories. Naturalists have always recognized that there are affinities between organisms, both plants and animals. It is better to use the word relationship, or indeed genetic relationship if this is known. Many classifications are purely arbitrary or artificial, giving us the term 'artificial classification'. Nevertheless, one important aim of modern classifications is to establish the true genetic evolutionary or phylogenetic relationships between organisms, that is, to establish a Natural System of Classification. In any case a classification of both plants and animals is necessary to the biologist if he is to form any philosophy of biology, otherwise his science becomes merely a jumble of numerous species. In a perfect system of classification species would be so closely connected to each other with little demarcation between them, and the concept of species would become superfluous.

In the Natural System of classification a new inference follows from the way the species are grouped. Varieties of a species are related by descent to a common ancestor or reticulately, species themselves are also related similarly and so on. This relationship implies that the variety is younger in time than the species, the species younger than the genus, the genus younger than the family and so on until we come to the phylum. Another point to notice is that while there are many species, there are fewer genera, fewer families, etc., until we reach the starting point which is the single kingdom. All classifications are logical, but some are more real than others. The classification of plants into trees, shrubs and herbs is a logical one and the categories are obvious to everyone, but they are not so clear cut; the demarcation is not always plain to see because, for instance, some shrubs may resemble trees. If our mind sees a connection between all herbs because they are herbs, and also between all shrubs and all trees respectively, the lack of demarcation between these units likewise suggests a connection between the three categories. And indeed there is a connection because they are all plants. When species, genera, families, etc., are examined and analysed in a similar way we can see quite easily how the earlier naturalists arrived at the idea of 'affinity' between species, because the classifications they invented were logical arrangements between the species. But, as species were largely regarded as immutable, affinity expressed a metaphysical rather than an empirical idea. As soon as the possibility that species were mutable was grasped affinity soon came to mean

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genetic affinity or blood relationship. Species were related because of a common descent and not by accident. A corollary is that species will vary directly according to the closeness of their blood relationship—the closer they are the more they will resemble each other. Good examples of this expectation is seen in the case of sibs (brothers and sisters), who are more like each other than non-sibs, or better still in uniovular or identical twins who are often so alike that they can be separately distinguished only with difficulty. A conclusion is that resemblances may be true indications of degrees of relationship which vary with the closeness of the resemblances.

This conclusion is justified on the basis of the examples given, but nevertheless it may be limited in the extent to which it may be applicable in the living world. Our conclusion gives us a generalization, but not necessarily a universal generalization. J. S. L. Gilmour,¹ however, pointed out that from a philosophical point of view both artificial and the Natural Classifications are concepts of the classifier and neither has more reality than the other. In this regard we may quote him as follows:

To sum up, starting from basic epistemological considerations, we are led to the view that a natural classification of living things is one which groups together individuals having a larger number of attributes in common, whereas an artificial classification is composed of groups having only a smaller number of common attributes; further, that a natural classification can be used for a wide range of purposes, whereas an artificial classification is useful only for the limited purpose for which it was constructed; and lastly both types are created by the classifier for the purposes of making inductive generalizations regarding living things.

Still, in so far as the Natural Classification approaches closer to a true genetic expression then it gains greater reality. In any case a true genetic relationship could only be experimentally demonstrated in few cases.

The importance of a natural classification lies in the fact that within the genus it is often demonstrably true, as modern research has proved beyond doubt, that species are often in fact genetically related. The classification based on known genetic relationships generally follows that based on resemblances and differences.

¹ 1940, p. 463.

Indeed doubtful points are often cleared up as research at a deeper level than that usually practised in classification is pursued. A good example of this is shown by the use of cytology in connection with classification giving rise to what is now called cyt-taxonomy. The systematist who is attempting to trace evolutionary patterns should also be capable of making use of cytology, genetics, ecology and anatomy, besides morphology. In cytology, the chromosomes form the obvious basis for comparisons of species because the number of chromosomes is constant in any one type, but differs regularly from type to type. Furthermore the chromosomes themselves possess an individuality, or morphology, such as size, number of constrictions, presence of trabants (satellites), which renders possible the description of a complement or set of chromosomes in the cells of a species. This description is called the karyotype, and karyotypes may be compared from species to species or from genus to genus.

A beautiful example of the correlation of the chromosome complement and the external appearance is seen in the primary trisomics of *Datura stramonium* discovered and described by A. F. Blakeslee and Blakeslee and J. Belling.¹ In the Jimson Weed (*Datura*) the normal or diploid number of chromosomes is 24, that is $2x=24$, and in it each chromosome is represented twice. A trisomic is an organism which has an extra chromosome, that is $2x+1$, in which one of the chromosomes is represented three times. The basic number in *Datura* is twelve chromosomes; thus there are twelve possible trisomics in this species. Blakeslee and Belling were able to obtain all of these twelve trisomics and could identify them by the form of their capsules which are very distinctive and enabled Blakeslee to name them as follows: globe, poinsettia, cocklebur, ilex, echinus, rolled, buckling, glossy, microcarpic, elongate, reduced and spinach. These various forms are illustrated in Plate 2. There were other differences in these plants. Classification of these forms obviously bears a close relationship to the internal composition of each. Other examples of trisomics have been described.

It is clear that the systematist can do only a limited amount of actual breeding work, but he may appeal to the work of the geneticists for confirmation of his classifications to a limited extent and in fact the modern systematist, who is tracing

¹ Blakeslee, 1930; Blakeslee and Belling, 1924.

evolutionary patterns as distinct from a classification alone, does make use of the results of other branches of biology. The use of anatomy in classification and in the determination of species differences has been shown in great detail by R. Florin who investigated the cuticular and stomatal apparatus of a large number of living and fossil members of the Coniferales (cone-bearing plants) and similar plants. Given only a very small piece of a leaf of a conifer it is quite possible to identify it. Florin found that the characters of the stomatal apparatus helped to separate taxonomic groups of high rank. He found that the anatomy and ontogeny of the stomatal apparatus formed a combination of characteristics which, at least to a certain extent, reflected the relationships of the orders or classes of gymnosperms. And along with the cuticular analysis the epidermal characteristics helped greatly to distinguish between genera, and sometimes natural groups within genera, and even between the species themselves. All told these characteristics were found to be important in developing a natural classification for the gymnosperms.¹

A few examples will illustrate the importance of these characteristics. The adult leaves of the English Yew (*Taxus baccata*) and the New Zealand Miro (*Podocarpus ferrugineus*) are linear, acute at the apices and spirally arranged in two rows. They are indistinguishable morphologically, but their epidermal features are quite different in several respects of the stomata and associated cells (see Plate 3). A new '*Taxus*' was discovered in China with leaves like *Taxus* but the male flowers were slightly different from those of the normal *Taxus* and the seed was white instead of red. Examination of the epidermis showed it to be distinctly different from *Taxus*, so much so that Florin could put it into a new genus called *Nothotaxus*. Another Chinese '*Taxad*' called *Amentotaxus argotaenia* was first placed in the genus *Podocarpus*, and then in the genus *Cephalotaxus*, but it is different from both. In fact the structure of its epidermis is unique among conifers and taxads which puts it into a new genus immediately (*Amentotaxus*, see Plate 3). Again, the 'living fossil' *Metasequoia glyptostroboides*, found only a few years ago in China, has vegetative shoots resembling those of *Taxodium distichum* (the Mexican Cypress) and also those of the juvenile condition in *Glyptostrobus* (Chinese Deciduous Cypress), but the leaves are decussate. The male

flowers are arranged in long terminal panicles as in *Taxodium*. The female cones have decussate scales but otherwise are like those of *Sequoia* (the Redwood), and, as in this genus, there are two cotyledons. Thus *Metasequoia* presented quite a problem to systematist and evolutionist alike. But the stomatal apparatus sorted the matter out a little. Examination of the apparatus shows that *Sequoia* and *Glyptostrobus* are not very far apart, but the structure of the stomata in the other genera is different. *Metasequoia* differs from all of them in the stomata and is so characteristic that it is possible to identify even isolated leaves.

Classification and systematics also find great support from ecology. The species rarely lives naturally in isolation; it is always a member of a population, and furthermore the pattern of variation finds its best expression in the population. Species also have a distribution in time and in space. Thus the ecologist nowadays is coming more and more to the aid of the systematist. J. C. Willis in his *Age and Area* theory¹ found that age alone in a species accomplished nothing, but age considered in relation to distribution of the plants led to several conclusions. Thus he considered (a) that the age of a species, or group of species, could be determined by estimating the size of the group as shown by its numbers and by comparing its size with that of others, and (b) that the age of a species is directly related to the size of its area of distribution. Many criticisms, however, have been advanced against Willis' theory, but nevertheless he pin-pointed the type of support to be given to the systematist by the ecologist. Statistical studies of the individual or grouped characteristics made on plants and animals obtained from many populations lead to the recognition of local races, the limits and extent of variations, the relation of the species to the genus and so on. There is a wide literature on this type of work and we can do no more here than mention a few names such as Turesson, Turrill, Huxley, Clausen, and Gregor. Readers who wish for further information on this rapidly expanding and interesting *rapprochement* of various categories of biological work which has even led to such new disciplines as 'experimental taxonomy' (Clausen, Keck and Hiesey)² or 'biosystematy' (Camp and Gilly)³ should consult Stebbins,⁴ Huxley⁵ and Turrill.⁶

¹ 1923, 1940.

⁴ 1930.

² 1934, 1940, 1944, etc.

⁵ 1940.

³ 1943.

⁶ 1931a.

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As a whole this modern work on systematics, using the help of other workers, has already shown that in nature there are many distinct species which are not separated by morphological characteristics alone. True classification must, therefore, expand its boundaries. A good example of this has been given by Dobzhansky¹ in *Drosophila pseudo-obscura* in which there are two morphologically indistinguishable races. Race A prefers a hot summer in Mexico, the Rocky Mountains and the coast of San Francisco, while Race B prefers the more temperate climate of the coasts of the U.S.A. and Canada, Sierra Nevada. Hence the territories of these two races overlap and while they may cross with each other, the hybrids are sterile. Dobzhansky found that at high temperatures Race A lays more eggs than Race B, but at lower temperatures Race B lays more eggs than Race A. These differences apparently are determined genetically because outwardly and in their chromosomes Races A and B are identical and they could only be distinguished by statistical analysis of characters such as size. Tan,² Dobzhansky and Sturtevant³ later showed that the differences between them lay in a large number of chromosome inversions in the two races.

It should be pointed out that in the opinion of many biologists varieties and species are considered to exist as actual natural entities, while the genus is an artificial category. W. H. Sharpe⁴ remarked that it seems to be impossible at present to give a definition of the genus which would be acceptable by various kinds of biologists. While artificial and natural systems of classification are logical constructions provided they use criteria which are essentially characteristic of the organism concerned, it is realized that it does not thereby follow inevitably that morphologically closely-related species are also closely related by descent except in cases where blood relationship has been shown by direct means. Still, the position is such that most biologists believe a natural system indicates common origin, or origin by descent, of the units which are classified. There is some diversity of opinion, however. For instance, W. T. Calman,⁵ writing from the point of view of a museum taxonomist, pointed out that although there is a very large number of animal species, about three-quarters of a million or more perhaps, he and his colleagues examine new species every day but they can nearly always put

¹ 1935. ² 1935. ³ 1938. ⁴ 1940, p. 337.

⁵ 1940, p. 435.

them into their place in the classificatory system. The unexpected species is a rarity; the species examined seem to run in well-defined channels. Calman wrote: 'As a result of this experience, we come to have a confidence in the Natural System of classification that is perhaps not always shared by our colleagues in the laboratory. The *Systema Naturae* becomes for us an objective reality, not a mere convenient filing device.' He believes that the Natural System is founded on descent with modification.

In the same way T. A. Sprague¹ as a botanist considered that natural classifications are truly phylogenetic and that experienced botanists came to this conclusion by a study of correlated characters. His explanation could scarcely be bettered and it shows the strength of the view that classification furnishes strong evidence for evolution. Hence we quote a chief passage:

If a natural classification in biology were merely 'a particular example of natural classification in general', why should characters previously unknown and unconsidered so frequently prove to be correlated in the same way? If, on the other hand, the 'natural' groups previously recognized are truly phylogenetic, there is every reason to expect such correlation. The fact that piece after piece of 'natural' classification has been strengthened by the discovery of additional correlated characters carries conviction to those most concerned. The taxonomist accordingly accepts the working hypothesis that the well-tested 'natural' groups in biology are phylogenetic, and this seems more scientific than to reject this hypothesis without offering any alternative explanation of the observed facts.

Sprague was careful to point out, however, that above the species rank phylogeny is mainly a question of probability, and that so-called phylogenetic trees of the angiosperms (the flowering plants) are purely speculative. On the other hand, J. S. L. Gilmour who examined taxonomy from a philosophical point of view, reported that there were two schools of thought generally among biologists, that is, one which considers the Natural System is 'one based on the phylogeny of the groups concerned' and the other doubts whether a logical classification 'is always and necessarily a phylogenetic one'. Gilmour also considered that probably phylogeny itself is a subsidiary system of classification which may be used as a background to the Natural System.

¹ 1940, p. 442.

In conclusion we may say that classification is an immense aid in biology and its value increases if it is considered also to show a true natural relationship between the organisms classified. Inasmuch as we do know without doubt that closely related forms do show close similarities we may reasonably extend this fact into a generalization and consider a true classification as a line of evidence for the occurrence of organic evolution. It is not, however, a proof of evolution and evidently could not stand by itself—it is a pointer towards evolution.

(c) *Evidence from embryology and serology*

(i) *Evidence from embryology*

It is convenient to group these two lines of evidence together under one heading. Neither of them makes the appeal now which it did in the earlier Darwinian period. As regards the embryological evidence the changeover in opinion may partly represent a reaction following on the exuberance and the undoubtedly exaggeration of the early Darwinians. For nearly fifty years the so-called biogenetic law dominated and was indeed the *raison d'être* of embryology to the sad neglect of more fundamental embryological research. One of the most famous and often quoted phrases in all biology is that which sums up this biogenetic law as 'ontogeny recapitulates phylogeny'. The history of those post-Darwinian years under the influence of Haeckel is a good illustration of how enthusiasts may be led away by wishful thinking and it does not stand to their credit.

Even in 1894, however, Gegenbaur¹ declared that ontogeny had become a field allowing full and dangerous play to an active imagination, and he maintained then that the necessary critique for ontogeny must be drawn from some other source outside the subject. By the turn of the century more and more biologists were beginning to realize that there was a tendency to exaggerate the importance of the biogenetic law (see Ainsworth Davies).² The search for evidence of recapitulation equalled in intensity that for the missing link. Even in modern times we sometimes read that the facts of embryology *only* permit an interpretation based on an assumption of evolution, no other interpretation being *possible*. The language of the evolutionary embryologists used often to be

¹ 1894, p. 5. ² 1902, Vol. 1, p. 9.

most picturesque and exaggerated; for example, J. Huxley¹ once described the human embryo as 'an imperfect memory' of a fish-like stage. Huxley, however, now rejects the law of recapitulation.

In order to appreciate this line of evidence it is necessary to outline some of the early stages of the development of organisms from the time of fertilization. In the usual form of reproduction (usual because it is common but by no means inevitable), a male sex cell, or gamete, unites with a female gamete. This process is called fertilization, and the product of fusion of the two gametes is called the zygote (and there are different kinds of zygotes each with particular names). Throughout the world of living things this process of fertilization varies considerably. For example, the bodies which fuse may not be gametes in the strict sense of the word—in the alga *Spiragyna* the whole contents of one cell fuse with the whole contents of another cell; or, again, in many fungi the fusion is rather between nuclei than between either gametes or cells. Nevertheless the fusion of formed gametes is essentially the method of sexual reproduction which predominates among organisms, especially the higher animals. Here we will only state some early features of the embryology of some plants and give a few other examples, otherwise we will deal chiefly with the facts as found in many animals.

In plants, among liverworts, mosses, ferns and fern-allies, that is, among all plants which possess an undoubted archegonium, which we mentioned earlier, after fertilization the zygote divides into two cells by a transverse wall and then into four cells by walls at right-angles to the first and next into a small ball of eight cells by walls at right-angles to the first two sets of walls. Some variation is found in this characteristic formation of the *octant*, as the ball of eight cells is called; for example, in *Selaginella* the zygote divides into two cells, one of these becoming an absorbing cell called the suspensor while the other forms the octant. The cells of the octant are so arranged that they form two tiers of four cells each and from the cells of each tier a specific tissue ultimately develops. Thus in all these plants the early embryonic stages are essentially the same and on evolutionary ideas this fact would argue a community of origin.

Some workers have considered that plants are particularly favourable as a source of examples of the biogenetic law because,

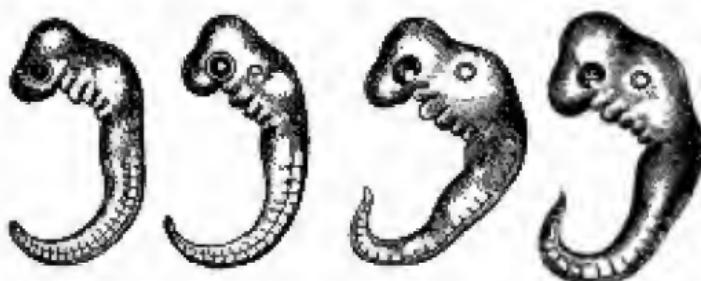
¹ 1934, p. 70.

unlike many animals, they have no free larval stage. In many cases structures are found in a young plant which do not occur in the adult plant but are found as normal structures in the adults of related plants. This applies particularly to leaves; for example, many cacti which grow in very dry situations are leafless, or have leaves which are extremely reduced, but in their seedling or early stages normal seed-leaves are formed. An unusual example is shown in the case of *phyllodes*. These are flattened stems which have taken over the function of normal leaves, or *phyllodes*. In the seedling stages most phyllocladous plants show normal phyllodes. In many conifers the primitive condition of the leaves is to grow directly on the stem. In the Scots Pine the normal leaves of the adult plant occur in pairs on dwarf shoots, but in the seedling up to the end of the first year all the leaves grow directly on the stem. There are many other examples which are sometimes considered to illustrate the biogenetic law (see E. C. Jeffrey).¹

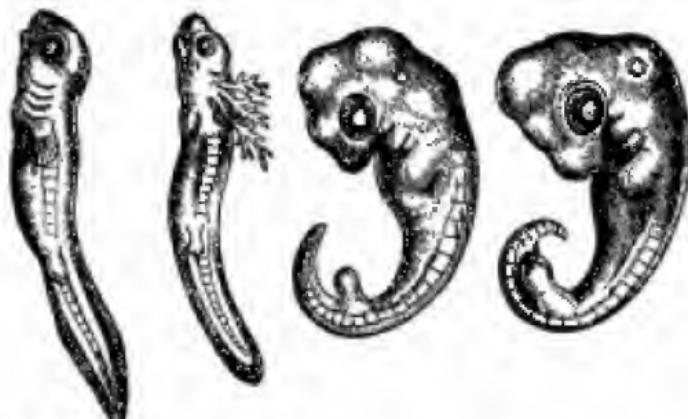
Among animals the story of recapitulation is much more complex because embryology is rather an epigenetic process as contrasted with the 17th- and 18th-century idea of preformation. That is, it is a process in which the young organism develops part by part and not a process in which a homunculus or mannikin in the egg merely unfolds and grows, as it were. This idea of epigenesis was in a sense one of the points which made the biogenetic law seem so convincing. The successive stages in evolution from fish up to man were exemplified by additions to the embryos in the more advanced stages. A bird and a man, therefore, would be fish-like because their embryos possess, or were said to possess, a fish-like stage. And indeed, comparisons of embryos of various vertebrate animals gave great support to this idea that the organism in its development, or ontogeny, goes through its evolutionary history, or phylogeny. Compare, for example, the embryos shown in Figure 3. At an early stage they all look alike, but later they begin to diverge each into its own characteristic type. It takes an expert embryologist to distinguish superficially between the early stages of, say, fish, salamander, tortoise, chicken, pig, calf, rabbit and man. Even von Baer, one of the founders of embryology and before Darwin's time, had two small embryos and he was uncertain whether they were lizard, bird or mammal. The stages shown in Figure 3, however, are not the

EVOLUTION AND CHRISTIANS

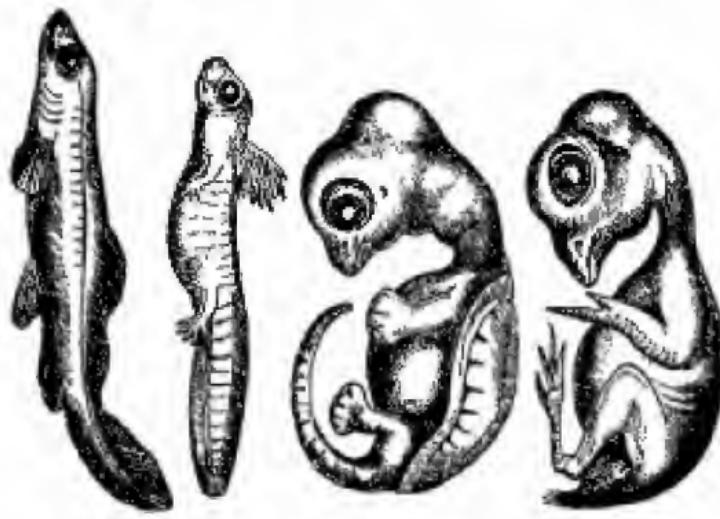
STAGE I



STAGE II



STAGE III



CLASSICAL EVIDENCE OF ORGANIC EVOLUTION

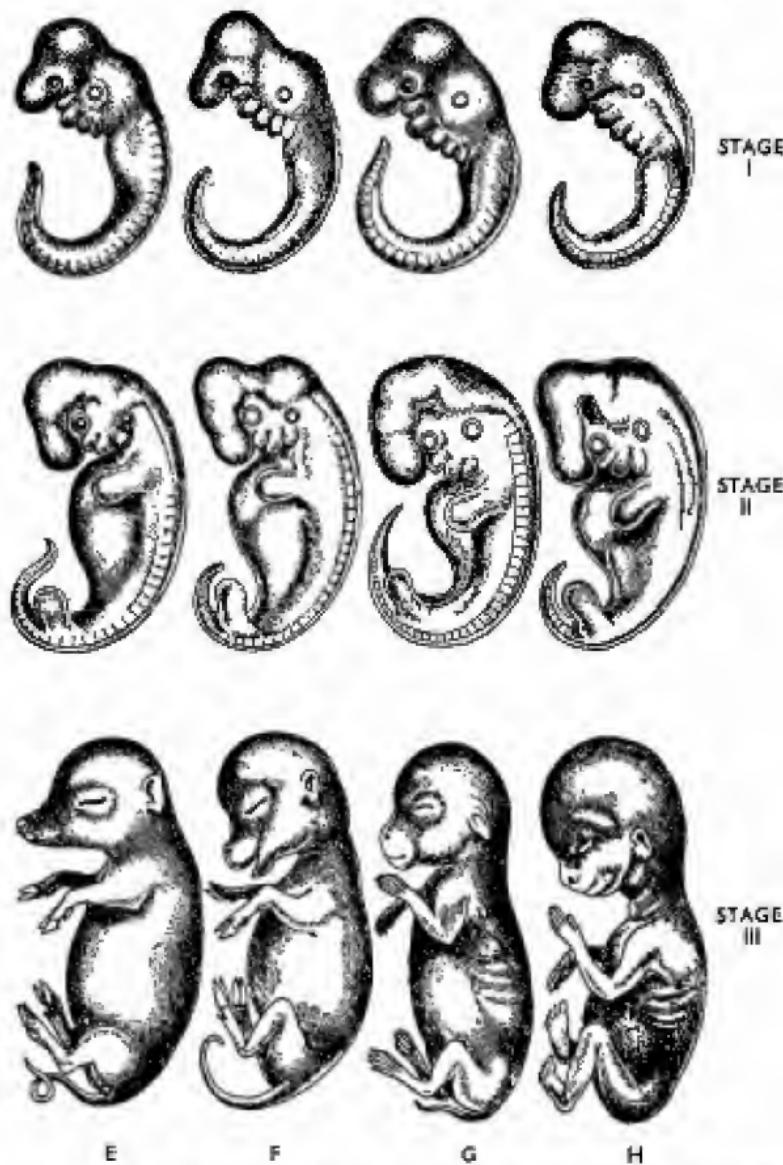


Fig. 3. A series of embryos at three comparable and progressive stages of development (I, II, III) representing vertebrate classes. A - fish, B - salamander, C - tortoise, D - chick, E - pig, F - calf, G - rabbit, H - man. (From Romane, 1893.)

earliest stages, however much they look alike, and it is important to realize, as Waddington¹ pointed out, in their very earliest stages the embryos of different animals are radically different.

We may note some of the recapitulatory features which animals are said to show. For example, the embryos of reptiles, birds and mammals show a number of gill pouches on the side of the neck in the position in which the gill slits occur in the adult fish. A pouch is not a slit, however, and it would be truer to say that these pouches resemble gill pouches in the fish embryo rather than in the adult fish. Further, internal to these pouches there are the blood vessels or gill arches which are disposed to the heart exactly as in the fish embryo. The heart itself in the embryo of these higher vertebrates is two-chambered like that of the fish. Again, all vertebrate embryos have tails which are very much alike in the youngest stages but which change as development proceeds, to become, as the case may be, a true fish tail, a mammalian tail and, of course, none in man. But occasionally a vestige of a tail is seen in man (see Plate 1). In the lower vertebrates like *Amphioxus* there is a primitive notochord (a rod-like structure which is the first part of the skeleton to be laid down); in fishes various stages in development of this structure are found, while in amphibians, reptiles, birds and mammals part of it develops to become the backbone. In the vertebrates three kidneys develop in the embryo in a set order; these are the *pronephros*, the *mesonephros* and the *metanephros* or fully-formed kidney. In the adult fish the process of development stops at the mesonephros stage.

Other types of examples which are quoted in the literature may be mentioned. The Rhizocephala *Saccoglossa* in the adult stage consists of practically nothing but a digestive and a reproductive apparatus, but in the larval stage it is a free-swimming *Cirripedes* form. Again, a flat-fish like the turbot, plaice or sole, lies on the bottom of the sand or mud on one side with two eyes on the upper side. But in the young stage these flat-fishes are symmetrical in form like ordinary fish with an eye on each side of the head. In an echinoderm called *Asterias* (the feather star) the adult consists of about ten waving feathery arms by means of which it can attach itself to rocks. But in the young state it is like a sea-lily rooted to the rock and with a long stalk to which the feathery arms are attached. Later the upper part with the arms breaks off

¹ 1916, p. 9.

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and swims away. The embryo of the Norwhale possesses a complete dentition in the gums and some other toothless whales also have embryonic teeth. By making use of embryological facts of this kind zoologists have been able to solve several problems of classification. The tunicates and *Balanoglossus* have been said to be related to the vertebrates. The King-crab was once thought to be a member of the Crustacea but embryology indicates that it is possibly really related to the spiders and scorpions.

We can appreciate how many facts of this type seemed to present convincing evidence of recapitulation. No other explanation of the likenesses of the embryos other than the straightforward one of relationship through evolution could be given in the earlier Darwinian period. It seemed to be so logical and reasonable to assert that if fish, reptile, bird and mammal evolved in that sequence then the occurrence of fish-like stages in the embryology of higher types was merely an illustration of an evolutionary path. This is a circular argument, no doubt, but one which was strongly held for many years. Whether recapitulation is evidence of evolution or not, the resemblances of these structures still require an explanation.

While it is undoubtedly true that many of these animals do look alike in their young stages, it should be pointed out that generally speaking it is the embryonic forms which resemble embryonic forms and not the embryo of a higher form which resembles the adult of a lower form even as von Baer stated before Haeckel's time. It is really a truism to say that the young of animals resemble each other more than do the adults. A basic postulate of the biogenetic law was that the animal embryo shows certain features of its phylogenetic past which, however, are useless to it as it develops and so are ultimately lost. In other words such structures as the tail in the embryo of man, or the gill pouches, are vestiges of a past stage. This uselessness is, however, an assumption rather than a fact. Among the cases already given W. R. Thompson¹ pointed out, for example, that, as far as *Sacculina* is concerned, a free-swimming larva is vitally necessary to the animal in order to find a host on which to spend its adult life. It is not a vestige, Dewar² and Dewar and Shelton³ showed very convincingly that many of these vestigial organs are present in the embryo not because they are recapitulations, but because they perform some

¹ 1927.

² 1931.

³ 1947, pp. 209-210.

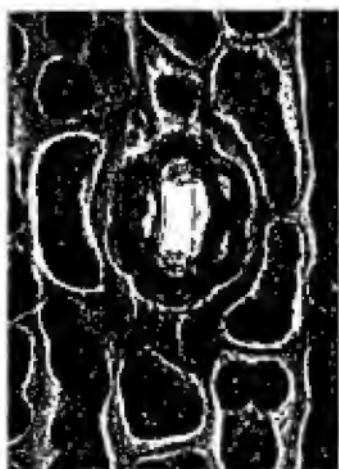
vital physiological function necessary to the animal in the stage and environment in which it is living. Dewar's¹ explanation of the presence of the three types of kidney in higher vertebrates will suffice to show us that an explanation can be given for all such structures on the basis of utility. We quote the passage in full:

As a kidney is a *size que non* of existence at a very early stage of embryonic development, long before a complicated one has time to develop, a very simple kidney, the pronephros, is first formed. This consists of a row of two or three nephridia on each side of the body. These nephridia are minute tubes, one end of which opens into the body cavity and the other into a common duct running the length of the body leading to the exterior. Each nephridium comes into contact with a bunch of tiny blood vessels known as a glomerulus. The waste products of the body are taken up from the blood by these nephridia and pass into the common duct and so out of the embryo. As the embryo grows, new nephridia arise behind the first ones. These are of more complicated nature and so are described as a second kidney, the mesonephros. As these increase in number the simple pronephros disappears. A kidney of the mesonephros type suffices to carry off the excretory products of a comparatively simple animal, and therefore persists in fishes as the permanent kidney. But a mesonephros is inadequate for the needs of more complicated animals, in consequence a far more elaborate kidney, known as the metanephros, is developed behind the mesonephros. When at last this kidney is ready to function, the nephridia of the mesonephros become absorbed, but their common duct persists and is used to convey male genital products. Thus, in my view, these three successive kidneys are a necessary and beautiful device for meeting the needs of the embryo while the final type of kidney is being developed.

We may note further that this example of development shows how efficient and economical Nature is in such processes of development. Nature does not waste structures. The mechanism underlying such embryological processes must be very finely balanced.

The germ-plasm layer theory of embryonic development probably began with Caspar Friedrich Wolf (1733-1794) in the 18th century, and developed until the time of von Baer (1792-1876) who crystallized embryological knowledge in this regard by recognizing that germ layers are present in many invertebrate and

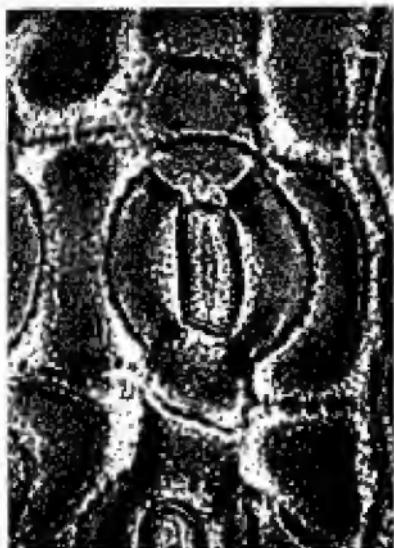
¹ 1947, pp. 209-210.



A



B

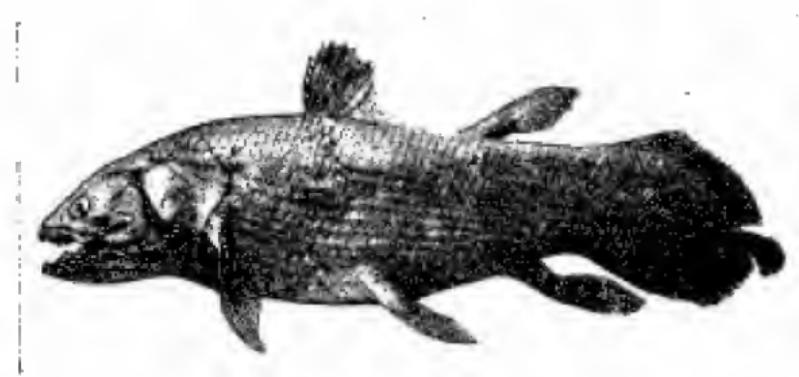


C



D

3. Types of gymnospermous stomata. Compare A (*Taxus baccata*) with B (*Podocarpus ferrugineus*) and C (*Cephalotaxus fortunei*) with D (*Amentotaxus argotaenia*). Note in each case the shape of the stoma and of the encircling cells. (From Florin, 1931 and 1932)



4. The Coelacanth. (From Smith, 1936)

vertebrate animals. Kowalewski¹ first showed in 1867 how a single-layered condition in *Amphioxus* became converted into a two-layered condition. Thus, soon after Charles Darwin published his *Origin of Species*, the sequence of changes in the egg and early zygote in many animals was known. Stated in a general way this sequence is described below, although of course there are many variations in different types of animals.

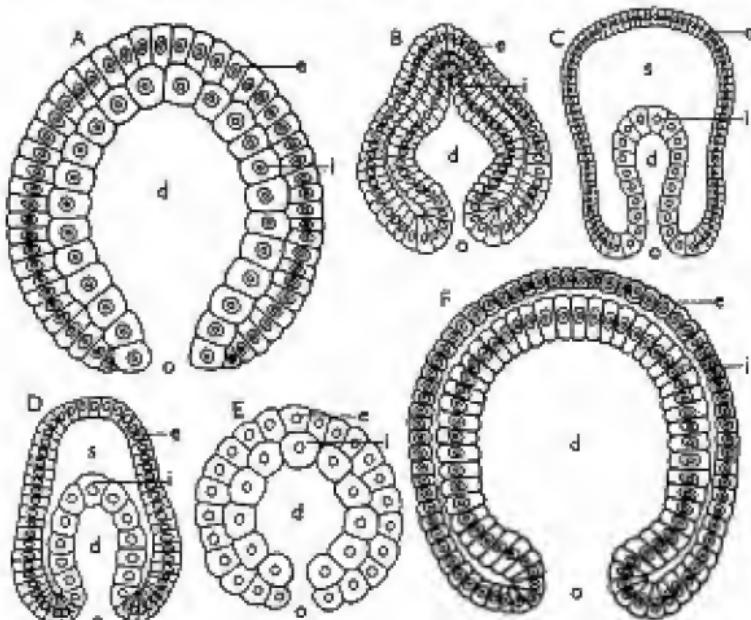


Fig. 4. Gastrulation. A - gastrula of *Gasteroplymmus* (a zoophyte), B - of *Sagitta* (a worm), C - of *Ureter* (an echinoderm), D - of *Nannipus* (an arthropod), E - of *Limnaea* (a mollusc), F - of *Amphioxus* (a vertebrate); d = intestinal cavity, o = primitive mouth, e = cleavage cavity, i = endoderm, e = ectoderm. (After Romanes, 1893.)

Fertilization occurs and this process consists of two distinct features. First the sperm nucleus unites with the egg nucleus and secondly the sperm activates the resultant zygote and sets in motion the subsequent cleavage changes. After fertilization the zygote begins to cleave, or divide, first into two, then into four, eight, sixteen, etc., cells until a small ball of simple, apparently undifferentiated, cells is formed. A liquid is secreted internally from

these cells so that gradually this ball is converted into a hollow sphere with the liquid in the centre. This stage is called the *blastula*. The blastula has only one layer of cells. Next, a part of the wall becomes invaginated towards the remaining part of the wall, or sometimes new cells are formed inwardly from the blastula wall. The resultant is called the *gastrula* which now consists of a hollow body with a two-layered wall and open at one end (see Figure 4). The outer layer of cells is called the *ectoderm* (*ectoblast*) and the inner layer is the *endoderm* (*endoblast*). Next a third layer of cells called the *mesoderm* is formed between the ectoderm and the endoderm. Finally the mesoderm becomes two-layered with a space or *coelom* separating the layers. Up to this stage the various cells of the embryo have been relatively undifferentiated but they become folded and poached out in various ways. From this stage onwards, however, the cells gradually differentiate until finally the tissues of the embryo are laid down. Thus the important stage is gastrulation and Nelsen¹ defined this as follows: 'Gastrulation is the dynamic process during which the major, presumptive organ-forming areas of the blastula become rearranged and reorganized in a way which permits their ready conversion into the body plan of the particular species.'

It has long been recognized that even in the blastula stage certain parts of the embryo constitute organ-forming areas. Special techniques are used to trace out developments of this kind, and for higher types Nelsen² listed the following areas in the blastula as: (a) a neural plate area in the ectoderm which gives rise later to the neural tube, optic nerves, retina and peripheral nerves, etc., (b) an epidermal area in the ectoderm which gives rise to hair, nails, scales, lens of the eye, sense organs of the peripheral part of the body, etc., (c) an endodermal area giving rise to the lining of the gut and other linings, (d) a notochordal area which gives the notochord, primitive antero-posterior skeletal axis, etc., (e) mesodermal areas giving the muscles, blood, kidney, uterus, gonads, etc., and (f) a germ-cell area which gives the primordial germ cells.

We note here that animals begin life as a single cell, but many of the lower forms, such as the Coelenterata (like *Hydra*), never get far beyond the initial stages. The trend of development is

¹ 1953, p. 390.

² 1953, pp. 333-334.

from the general to the particular. In 1872 and 1874 Haeckel developed his blastaea-gastraea theory. He gave the name gastrula to the two-layered embryonic structure and he likened it to the adult coelenterates, although in these types the blastula is not formed by invagination but by a process of delimitation from the dermal layers. The body of these animals was said to be made up of two layers enclosing a central cavity, or enteron, with an opening or mouth at one end, and at this end two-layered cavity-less arms or tentacles grew out. Haeckel postulated a primitive adult form, or blastaea, with a similar structure to the blastula, i.e., it was made up of a hollow ball of cells filled with fluid and with cilia growing out from the wall. Next he conceived that from this arose a further primitive adult type also with cilia and similar to the gastrula stage. From these postulated types he assumed the derivation of all subsequent forms of protozoa and metazoa. Hence the metazoa in their early stages went through the adult stages of their ancestors; in other words, they recapitulated their phylogeny. In this way Haeckel developed his biogenetic law which he then applied to all embryos.

One most far-reaching result of Haeckel's blastaea-gastraea theory was that many zoologists accepted the evolution of the metazoa from a coelenterate type of ancestor, which itself had evolved from protozoa. It is easy to see now that Haeckel's initial mistake lay in comparing an *embryo* with the *adult* of a postulated lower form, or in considering that the larval stage in development represented the adult condition of a previous ancestral form of animal. He also pictured changes occurring by the addition of structures to the embryos over and above those already there. But it is now well known (and had in fact been emphasized by von Baer before Haeckel's time) that embryos may resemble each other but an embryo never resembles an adult. And again, embryonic changes generally are not *additions* but rather *substitutions*, a new organ usually replaces an organ previously present. The development of the kidney gives an excellent illustration of such substitutions. Embryos tend to resemble one another at certain stages precisely because they are going through similar stages each in their own developmental cycles, and it is necessary for the embryo to work highly efficiently and smoothly while the complicated changes leading to the adult condition are taking place. There is a necessary ontogenetic

connection between form and function in the embryo. Waddington¹ summed up the modern position in these words:

The type of analogical thinking which leads to theories that development is based on the recapitulation of ancestral stages or the like no longer seems at all convincing or even very interesting to biologists. Our interests have been awakened by the possibility of an analysis of development in causal terms; and it is in this field that modern embryology seeks for its guiding principles. Recapitulation, in all the forms in which it occurs, remains an important phenomenon, but it appears nowadays as a series of problems for evolutionary theory to discuss rather than as an explanation of developmental processes.

If evolution takes place it must be connected to embryology in some way, even if it is the adult which actually evolves rather than the embryo, because both adult and embryo are the same individual. If recapitulation is not the guiding principle in embryology, or even of importance, it is possible that it has little value for evolution and less still as evidence for its occurrence. Analogies are only useful up to a certain point, if they are carried too far they may lead to error, as indeed the biogenetic law undoubtedly did in embryology and retarded progress for many years.

It has been pointed out by de Beer² that if embryology has any significance for evolution it will lie along lines indicating affinities between related forms, because the younger the embryos and the more closely related they are then the greater the resemblance between them and these resemblances persist longer between closely allied forms. If embryology is to furnish precise evidence for evolution it requires a rigid delimitation between *palingenetic* and *coenogenetic* characters in the embryos. Palingenetic characters are those which are derived from a long line of ancestors; while coenogenetic characters are those which have been more or less recently acquired by the embryo due to its needs in a changing environment. But these characters are so intermingled in any embryo that their determination becomes largely a matter of speculation and pre-conceived ideas.

G. R. de Beer has consistently opposed Haeckel's interpretation of embryology in an endeavour to obtain a causal analytic, rather than an historical, approach to the subject. He developed

¹ 1936, p. 10. ² 1928, p. 486.

his criticisms in detail in his book *Embryos and Ancestors* and we must give some of his conclusions which are important and are currently used in embryology. De Beer found that recapitulation does not occur; phylogeny has no causal relation to ontogeny because the ontogeny of a descendant is affected chiefly by inheritance from a previous ontogeny, while phylogeny is the result of inheritance and of external factors. By phylogeny de Beer means comparisons of adult forms and this is the method of palaeontology which is unable to investigate the ontogeny of ancient forms of organisms. Ontogeny, however, is the study of the development of organisms throughout their developmental period from fertilization onwards. De Beer wrote: 'Each ontogeny is a fresh creation to which the past contributes only the internal factors by the means of heredity.'¹ As the soma is more or less distinct from the germ-plasm then the adult form contributes little to succeeding ontogenies. But in the ontogenies changes may occur which may affect the appearance of succeeding adults by inheritance. Many of these changes occur by alteration of relative rates of development of various organs. Evolution, as de Beer said, results from 'the acquisition of qualitative novelties and by the production of novel situations by quantitative alteration of the rate of action of the internal factors'.² Phylogenetic effects are produced by (a) *paedomorphosis* in which youthful characters are introduced into the adult sequences by means of *deviations* from ancestral conditions and by means of *neoteny* or a retardation of the bodily structures while reproductive structures advance; (b) by *gerontomorphosis* or modification of characters already present in adult forms, through *adult variations* which are inherited, through *hypermorphosis* or delayed development and through *acceleration* in the young stage in which an ancestral character appears earlier than normally. Hypermorphosis and acceleration may produce *palaeogenesis*, or repetition of characters, present in ancestors. Palaeogenesis simulates recapitulation and de Beer pointed out (page 90) that the mistake of the recapitulationists was to consider that the repeated character represented the adult character of the ancestor when it may really be an embryonic or larval character.

De Beer's conclusions and the modern embryologist's views resulting from analysis of ontogeny in terms of causal relationship

¹ 1928, p. 35.

² 1928, p. 96.

has freed embryology from the 'mental strait-jacket' of recapitulation.¹ Thus phylogeny is seen as the *result* of ontogeny and not its *cause*. Phylogeny is an historical study of adult forms which does not give critical information of the decisive stages of ontogeny. Ontogeny depends ultimately on the genetic make-up of the organism and so de Beer can conclude: 'But since phylogeny is but the result of modified ontogeny, there is the possibility of a causal analytic study of present evolution in an experimental study of the variability and genetics of ontogenetic processes.'²

(ii) *Serology and biochemical evolution*

A more recent approach to evolution is through biochemistry, and while there is not as yet a great deal of correlated information available, the term biochemical evolution is an accepted one. Marcel Florkin's *Biochemical Evolution*, already mentioned, has brought together much recent information on this subject and some of the information given below has been obtained from this book.

Florkin finds that no matter what the classificatory position of an animal, there are undoubtedly biochemical similarities indicating a unity of biochemical design. Chemically, living things show many common properties. Water, of course, is common to all living things; a limited number of mineral substances seem also to be a *sine qua non* of organisms. The protoplasm of animals always contains sulphates, chlorides, phosphates and bicarbonates of potassium, calcium, magnesium and sodium. These substances are also characteristically present in what Florkin calls the true '*milieu interieur*' or biological fluid which in metazoa is found as a tissue lymph and an interstitial fluid. Again, the bulk of the dry residue of animals always contains large proportions of the organic substances, proteins, lipids and glucosides, along with the salts mentioned above. As proteins are ingested by animals they must subsequently be digested and the products absorbed by the body. Digestion of protein is invariably brought about in all kinds of animals by a series of enzymes which operate in the same sequence; these enzymes are the proteinases, carboxy-peptidases, aminopolypeptidases and dipeptidases which break down the proteins into polypeptides, dipeptides and finally into amino acids.

¹ De Beer, 1928, p. 93.

² 1928, p. 98.

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Smooth and striated muscles are a feature of vertebrates and of some invertebrates. A muscle works by contracting itself and thus exerts a pulling force on the distal part to be moved. This contraction takes place in all cases through chemical means involving a protein called actinomyosin and in which the energy necessary for the reaction is obtained from the anaerobic breakdown of glycogen which again follows the same path no matter what the animal. This path is as follows: glycogen is degraded successively to hexosemonophosphate, hexosediphosphate, triosephosphate and finally lactic acid.

There also seem to be orthogenetic trends in the evolution of the various biochemical systems in animals. For example, the amount of protein in the blood increases regularly as we pass from molluscs and gastropods to cephalopods; while on the other hand, the protein sugar content decreases in concentration as we travel up the animal scale to cephalopods. The efficiency of the blood in carrying carbon dioxide in animals increases greatly in the order gastropod, skate, turtle, goose, horse, man. There are other similar examples. What may be called a metabolic orthogenetic trend is well illustrated in the variations of purine metabolism as found in animals with different degrees of complexity.¹ The complete cycle of purine metabolism is as follows: adenine and guanine are two amino-purines found in animals, and these are first of all de-aminated to become hypoxanthine and xanthine respectively. Then both of these are oxidized to become uric acid and this is the end of the first stage. The next stage is called uricolysis and it consists in the breakdown of uric acid to allantoin, then allantoic acid, glyoxalic acid and urea. Finally urea is split into ammonia and carbon dioxide. This cycle is not completed in all animals, but a shortening occurs by the gradual loss of the end links in the chain as we pass up the animal kingdom. The complete cycle is found in marine invertebrates such as the mussel and crustaceans. In the fresh-water mussel, fishes and amphibia the last link is missing and the cycle proceeds only as far as urea; in higher animals, insects, reptiles, birds, and mammals the cycle only goes as far as allantoin or to uric acid.

In genetics there are a number of examples which show the synthesis of metabolic products as step by step gene changes, and in other cases mutations may vary from the parent by a gene

¹ Florkin, 1949, pp. 44-49.

difference. Hence chemical evolution may ultimately be dealt with at the gene level. We have already mentioned the chemical homologies and analogies which are to be found in the chemistry of animals, and sufficient has now been given to show the kind of evidence for evolution which biochemistry may be expected to furnish in the future.

Evidence of a similar kind is obtained from blood tests and we mention it separately here because it is generally treated as evolutionary evidence under the heading of *serology*.

Blood is a liquid tissue carried in blood vessels (in the higher animals) and forms a transportation system conveying oxygen, carbon dioxide and food to and fro between the body tissues. Essentially, blood consists of plasma or serum which contains salts, food and waste matter, and also of red and white corpuscles. Enzymes, antibodies, antitoxins and antithrombin are also present. As we have already mentioned there are four main colouring matters in blood giving four distinctive kinds of blood—red haemoglobins, green chlorocruorins, blue haemocyanins and red-violet haemerythrins. These are found in different animal groups. While in general the blood of animals may belong to these four analogous types, the blood of no two species of animal is absolutely identical. Blood is such a complex mixture and carries such an assortment of substances that it varies tremendously. The fact of this variation has been made use of by comparing the blood of different animals by means of sera or blood precipitation tests.

The technique of these serum tests is as follows. The colourless serum is extracted from (say) human blood and a quantity is then injected into a rabbit over a period of time. Because the human serum contains proteins which are not acceptable to rabbit blood, the latter forms an antibody which protects the rabbit from the human proteins. In this way a certain amount of antibody for human blood may be built up in the rabbit. If now this antibody-charged rabbit's blood is taken and the serum separated it is found that the serum contains the antibodies. This may be called anti-human serum, and if a few drops of it are added to human blood serum, the proteins may be precipitated. Such anti-human serum may be tested with the sera of various animals and according to the amount of the precipitation obtained a comparison may be made with human blood—the greater the precipitation the nearer

the blood concerned would be to human blood, at least as regards the protein content.

Elaborate tests of this kind were first extensively carried out on many animals by G. H. F. Nuttall in 1904. Nuttall and his co-workers carried out about 16,000 tests *in toto*. Since then other people have examined various types of blood as regards the precipitation tests and many claims have been made purporting to show the relationships of animals, but at the same time there have been many contradictions among the results. It has been claimed that:

- (a) Birds show blood relationship to reptiles.
- (b) Whales show relationship to hoofed mammals.
- (c) Lizards and snakes are closely related.
- (d) The King Crab is nearer to the scorpions than to the crabs.
- (e) Seals and sea-lions are related to dogs, cats and bears.
- (f) Llamas are clearly related to antelopes, goats and sheep.
- (g) Matsupials are related to the Tasmanian wolf.
- (h) Turtles are related to crocodiles.
- (i) All carnivora are more alike in their blood than other mammals.
- (j) Man, apes, monkeys, etc., show a closer relationship to each other than to other mammals.

It would seem that the evolutionary relationships indicated by these blood tests follows those shown on other grounds. But before a final conclusion is reached some of the contradictions brought out by the tests should also be considered. D. Dewar¹ has done this in detail and we give some of his findings. He found that Nuttall's experiments also showed some human beings are less closely related to their fellow men than to the anthropoid apes; some showed closer relationship to Old and New World monkeys than to their fellow men and again others seem to be just as closely related to carnivores, ungulates and rodents. One test showed that hooved animals were closest to the Cetacea but another test showed them to be most closely related to bats. Again, the crane had more affinity with the emu and the turtle than with the sparrow. While eel serum destroyed the red corpuscles of adult rabbits but not those of newborn rabbits.

¹ 1931, pp. 29-30; 1940, pp. 87-97.

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As blood is a limited tissue, limited in a chemical sense and in respect to function and also because of contradictions such as those mentioned above, it would seem to be better not to attach too great importance to blood tests as far as evolution is concerned. All mammals possess a backbone which no doubt is chemically the same in the higher ones at least but that is no reason for saying that they are therefore related. The backbone is part of the common structural plan of vertebrates in general, and perhaps blood too, as it is a tissue, with minor variations, is also part of that plan.

Chapter IV

The Classical Evidence for the Occurrence of Organic Evolution, Continued

1. EVIDENCE FROM PALAEOONTOLOGY

2. General accounts

MANY biological writers have emphasized the importance of the palaeontological evidence for the occurrence of evolution. Some consider it to be the only direct evidence we have inasmuch as the palaeontologist studies fossils as they occur sequentially in the earth's strata. Others, such as Dewar, consider that the whole theory of evolution stands or falls by the evidence from the rocks. He contended that if this evidence is complete the theory stands demonstrated, but if it is essentially incomplete the theory must be discarded, or used only as a working hypothesis, despite conclusions, or inferences, which may be drawn from other branches of biological science. In presenting the evidence for evolution from embryology we stated that phylogeny gives an account of resemblances only between adult (or at least formed) organisms; it tells us nothing about ontogeny or the individual development of organisms from the fertilized egg onwards. Palaeontology gives us a history of dead forms and it aims to construct the phylogeny of organisms which lived in the past, i.e., it attempts to show the morphological relationship, real or assumed, between past organisms and to connect these forms with their living representatives. Thus fossils by themselves can never furnish a rigid proof of genetic connections between organisms for the simple reason that the ontogeny of such organisms represented by the fossils is unknown and can never be known. A beautiful and complete series of fossil shells, for example, may provide us with an excellent evolutionary series in which one form grades into another. And it may in fact be true that each member of the series was evolved in turn from its immediate predecessor. On the other hand, it always remains possible that the likenesses between

the shells which enable us to construct the series is coincidental—the actual animals which originally inhabited the shells *may* have been different. A point such as this one may possibly be settled by turning to other departments of biology, such as comparative anatomy, where living forms can be examined.

What we wish to emphasize here is that while the evidence from palaeontology is of very great importance in evolution it is not absolutely conclusive, and can never be so in itself, because it must always be incomplete, not only because it may be geologically imperfect at any given time, but because the picture it gives us of the organisms concerned is necessarily only a partial one. The fossils, however, are the only factual material we have which give us any indication of what organisms were like in past eras in the history of the earth. They give us a certain pictorial history of the creatures which once lived on the earth and the knowledge gained from this aspect may be joined to knowledge gained from other aspects concerned with the evolution of living forms and joined also to the experimental and causal factors which we know affect and produce change in organisms. De Beer¹ pointed out that only a study of ontogeny (or similarity in ontogenies) gives proof of genetic descent and it is as well to state that the basic assumption behind the evolutionary study of fossils is that structural and morphological similarity indicates closeness of kinship. This is an assumption which follows from the biological principle of correlation (Cuvier). It is only by accepting this assumption that sense can be made of the myriads of fossil forms which have been found.

A fossil is the remains of any plant or animal, such as casts, im-pressions, petrifications and even footprints, found in the strata making up part of the earth's surface. There are two chief major kinds of rocks in the surface of the earth, (a) igneous rocks which were formed from molten matter such as lava and (b) sedimentary or stratified rocks which were laid down regularly layer by layer by deposition of particles chiefly in water and over a long period of time. The stratified rocks consist chiefly of limestones, sandstones and shales. Fossils are found only in these stratified rocks; any organisms involved in igneous rocks would be completely destroyed by the heat of the molten rock and no trace of them could remain when the rock had solidified. That the sedimentary

rocks (and the term rock in the geological sense includes anything in the earth's surface except the soil) are laid down in layers or strata is well known and obvious to anyone who visits a quarry. If the surface of the earth is stratified in this way it is clear that the lowermost strata would be deposited or formed first, i.e., they would be the oldest in time, while the uppermost strata would be younger.

The absolute age of the earth and of the strata thus becomes of importance but, until fairly recently, methods for estimating the age of the strata were inaccurate and unreliable. Modern methods chiefly involve calculations depending on the rate of radioactive disintegration of uranium and thorium to lead. Other similar methods have been tried out but are not so successful. The radioactive method was first proposed by Boltwood¹ in 1901 and gradually physicists and geologists came to realize that it is a fairly exact method capable of confirmation; for example, uranium 238 and 235 and thorium may occur in the same mineral and this allows for three separate estimations which should theoretically agree. As yet, however, not all rocks and strata have been investigated by these methods. It is still common practice to date a stratum according to the fossils it contains and in practice this method has proved reliable up to a point and it is certainly more convenient than the radioactive method. Of course, it does not give any indication of the age in years of the strata but it does indicate the sequence of the strata and the periods to which they belong. Gradually the absolute age, as far as this can be scientifically determined, is being worked out by the co-operation of the physicist, the biologist and the palaeontologist. An excellent and summarized account of the age of the earth has been given by A. Knopf.²

At one time one of the great difficulties confronting Darwinian evolutionists was the great length of time needed for evolution to occur and in Darwin's day estimates of the age of the earth were very conservative and relatively small. The new methods give the oldest rocks an age of at least 2,000 million years and A. Holmes³ stated that the age of the earth may be about 3,300 million years, while a recent figure by T. S. Westoll gave it as 3,500 million years.⁴ The first absolutely certain remains of organisms are found in strata laid down about 520 million years

¹ 1901.

² 1949, pp. 1-9.

³ 1947.

⁴ 1958, p. 236.

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ago.¹ This great period of time certainly eases the difficulties of accounting for slow evolution encountered by the earlier evolutionists. The chief divisions of the earth's crust which represent geological time are called *eras* and they are five in number—Archaean, Palaeozoic, Mesozoic, Tertiary and Quaternary. The first four are divided up into a number of *Periods* as

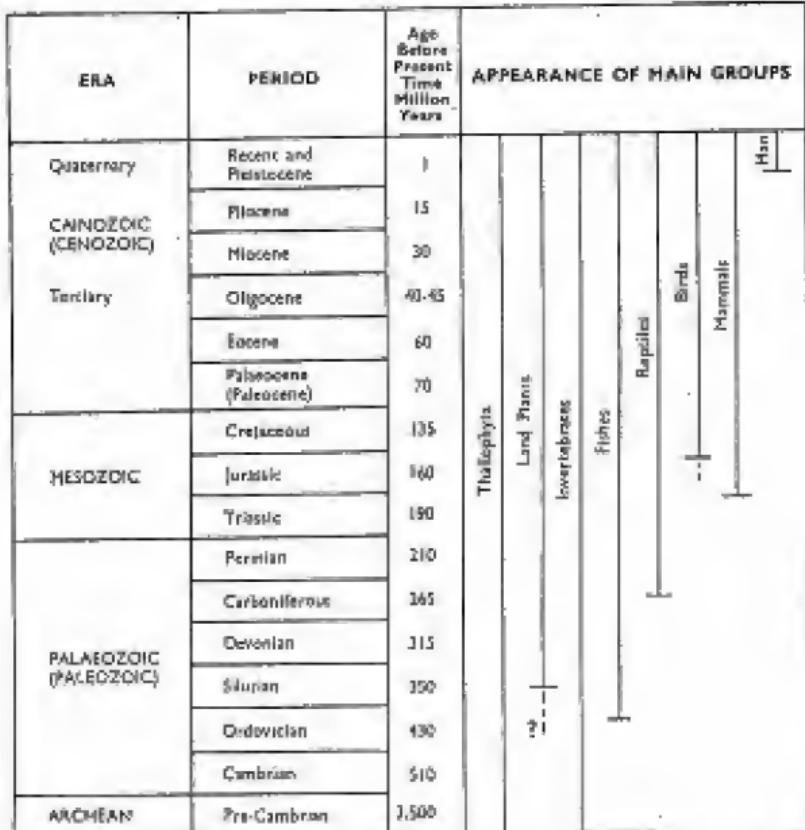


Fig. 5. Geological Eras and Periods with time scale in millions of years and main plant and animal groups. (Partly based on Westoll, 1958.)

shown in Figure 5, which also gives a modern estimate of their age in years and the main fossil groups which have been found in these rocks. Under normal circumstances these strata and their subdivisions always occur in the same order with the Archaean at

¹ Remains of possible organisms have been described from Archaean strata which may be 2,500 million years old; see page 110.

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the bottom and the Quaternary at the top, or surface of the earth. But, due to various upheavals of the earth's crust, nonconformities are sometimes found in which the order of the strata is altered, or even completely reversed. In all these cases, however, there is always good evidence to show that some upheaval has in fact produced the nonconformity.

One important feature about the strata which was first noted by G. W. Smith in the early 19th century is that each stratum contains its own characteristic fossils which are not always found in other strata. This discovery in fact formed the basis of paleontology. Some types of organisms seem to have been in existence throughout the whole of geologic time or nearly so since the first appearance of fossils from the Cambrian Period onwards; others were in existence near the beginning but have since died out; others again started relatively late and died out relatively early, while others yet again made only a fairly recent appearance in the rocks.

There must be millions of individual fossil plants and animals which have been found and many of them are preserved in museums, etc. Some parts of the stratified rocks show few or no fossils and others show very large numbers. For example, spiral ammonites occur in different rocks in very large numbers; the invertebrate echinoid *Micraster* is abundant in the English Chalk Beds. While Broom¹ described the Karroo Fossil Beds of South Africa as covering an area of about 200,000 square miles, almost every part of which showed the presence of fossils. He wrote: "The fossiliferous beds are of great thickness. In some cases they must be 4,000 to 5,000 feet thick; in others perhaps only 2,000 feet. It would be a very conservative estimate that would put the average thickness at 2,000 feet and at every few inches we have another page of the book and another series of fossils to be revealed. I thus estimate that in the whole Karroo formation there are preserved the fossil remains of at least 800,000 million animals." But up to 1932 only 1,200 skulls had been collected belonging to about 350 species. Broom considered that about a million fossils were just waiting to be picked up. Such an exceedingly fossiliferous formation, of course, is rarely found, but yet it shows that there may be many more fossils to be found in different parts of the world than we are sometimes led to believe.

¹ 1932, p. 308.

The numbers of genera and higher groups of animals found as fossils varies greatly throughout the strata. For example, the number of genera of molluscs, which have the largest number of genera of any animal group, started in the Cambrian Period and quickly expanded from then to about the Permian Period when the number of genera had decreased, only to expand again to a greater extent in the Cretaceous Period and they have persisted up to modern times. The Bryozoa, which have left a good fossil record, first appeared in the Ordovician Period in large numbers of genera which gradually decreased in number until by the time of the Triassic and Jurassic Periods there were only very few of them left, and then relatively quickly they increased to greater numbers than ever before up to the Tertiary Era. The number of genera of these animals now seems to be decreasing. The vertebrates, which are the last animal group to appear in the fossil record, have had several similar phases of expansion and retraction as regards the number of genera. J. Brough¹ gave a summary of the numbers of families of many animals throughout their geological history up to the present day, and we give a few of his examples. Among echinoderms there are 111 families of which fifty-one first appeared in the Lower Palaeozoic, twenty-two in the Upper Palaeozoic, twenty-eight in the Mesozoic and five in the Tertiary Eras. Only twenty-nine families exist at the present time. In the Mollusca ninety-eight families appeared in the Palaeozoic, 100 in the Mesozoic and two in the Tertiary Eras. Facts of this kind led Brough to consider that evolution in the past was different in some way to evolution at present. It was probably a much quicker process than it is today. He envisaged an early period when the phyla first formed and then later there were periods when classes and orders, etc., came into existence and the evolutionary process in general slowed down.

One of the outstanding features of the fossil record is the impression which a general survey of it as a whole gives. This feature indeed was realized from the early days of palaeontology and it is an impression of orderly increase from simplicity to complexity in the bodily structure of the organisms occurring as fossils. In general, there has been a more or less steady increase in the numbers of kinds of animals and plants from the earliest to the latest geological strata, and accompanying this increase in kind

there has been an increase in the diversity of form. Technically this feature of the fossils is known as a progression from homogeneity to heterogeneity. The animals and plants in the rocks seem gradually to develop more and more specialized features. Among animals, invertebrates become simple vertebrates and the higher animals appear in the order fishes, amphibia, reptiles, mammals, birds and man; while, among plants, aquatic algal plants appear first and land plants later in the order fungi, Pteridophyta, Bryophyta, flowering plants. Among animals this order is also an order of progression from simplicity to complexity, but among plants the order of appearance of the fossils is not so clear, and does not in fact agree with the order from simplicity to complexity. It is worth while discussing this important point in more detail.

On morphological and ontogenetic grounds plants, excluding the fungi, are generally arranged in an order starting from the simplest to the most highly developed, i.e., from algae to liverworts, mosses, Psilotales, horsetails, lycopods, ferns, conifers, monocotyledons and dicotyledons. In the rocks, the algae appear first and are present throughout all the Periods, then the Psilotales, which are land plants, appeared next in the Silurian Period with a possibility that they existed much earlier. Then horsetails, lycopods and ferns appeared, to be followed by liverworts; next conifers, monocotyledons and dicotyledons make their appearance, while the mosses appeared last of all. According to this order the time of appearance of liverworts and mosses is anomalous, because they are the simplest of all the archegoniate plants (i.e., bryophytes, pteridophytes and gymnosperms), and they should occur before the horsetails and perhaps even before the Psilotales. In fact the origin of liverworts and mosses is clouded in obscurity, although it has been suggested that they are a later derivation by reduction from some higher group of plants because they possess stomata which are so characteristic of higher plants. But the derivation of the Bryophyta from a higher group would involve a very fundamental change in the relative importance of the two generations which are found in the life history of these plants. As Scott¹ said: 'The absence of any geological evidence, however, makes the question of the origin of bryophytes an almost hopeless one.'

¹ 1924.

Nevertheless, except for the bryophytes, the general impression from the fossils is that the remaining plants appear in the order in which we expect them to do so if evolution has occurred. The aberrant bryophytes are a stumbling block in this respect, but judgment about them may be legitimately suspended because they are, on the whole, very delicate and small plants which perhaps do not easily fossilize. Among organisms which have hard parts and fossilize relatively easily, the fossil record does not show one example of a type of organism out of place in the evolutionary scale.

In the Proterozoic Period immediately before the Cambrian some fossils in the form of algal-like impressions, worm-casts or imprints of jelly-fish have been found. The great age and depth of these rocks renders it difficult to identify the fossils with much degree of certainty. Some of these older algal impressions were described by R. B. Young¹ and they furnish strong evidence that living things were in existence in Pre-Cambrian times. Even in some of the oldest South African Archaean rocks A. M. Macgregor² described the presence of supposed algal fossils and A. Holmes³ reported that the latest determinations of the age of the Bula-wayan System to which these rocks belonged was at least 2,600 million years. This means, as Holmes stated: 'that life has existed for at least 2,600 m.y. and probably for considerably longer than 2,700 m.y.'

Still, the complete absence of fossils of animals with hard parts in the Pre-Cambrian rocks is puzzling, unless indeed they were all soft-bodied and not suitable for fossilization. The absence of fossils in the Proterozoic, however, means that the early evolution of living things cannot be known with certainty. Palaeontologists and biologists normally consider the Cambrian fossils represent the descendants of those organisms living in the Proterozoic. The Proterozoic Era lasted for many millions of years. As already mentioned, undoubted fossils are first found in the Cambrian rocks which extend over a period of about 100 million years. All of the fossils were aquatic. The first plants were algae, or seaweeds, particularly those with a calcareous outside layer, while all the animals at that time were invertebrates spread over all of the most important phyla, such as sponges, jelly-fishes, sea cucumbers, starfishes, lampshells, molluscs and crustaceans, and also some worms. Thus, of the great divisions of the animal

¹ 1932, 1934.

² 1941.

³ 1954.

kingdom all were formed in the Cambrian Period except the Vertebrata, and these first appeared in the next, or Ordovician Period, in the form of pieces of bone called ostracoderms. One very noticeable and important fact regarding evolution among these earliest fossils is that all the phyla appear in the rocks formed, i.e., possessing the complete bodily plan of construction typical of their phylum. For example, the earliest crustacea are undoubtedly crustacea, the earliest molluscs are undoubtedly molluscs and so on. In fact, at the first appearance in the rocks of any member of the plant and animal phyla, they were just as clearly and distinctly separated from each other as they are today. In other words, the phyla appeared 'suddenly' as it were, giving among their fossils no indications of their origins from other phyla.

According to the theory of evolution these phyla should have evolved one from the other in an increasing scheme of complexity and diversity. They should grade into one another at least to a much greater degree than they do at present. There should be fossils which connect the phyla unmistakably, but none have been found in the early rocks. Even in the case of the vertebrates which appeared last among animals there is no true connecting link with previous phyla, with the result that there is no unanimity of opinion regarding their origin. As the anatomists Neal and Rand¹ said: 'One of the many unsolved problems of biology is that of the ancestry of vertebrates.' These workers in fact looked for the origin of the vertebrates from some of the earliest invertebrates and not from any of the existing types, except perhaps the protozoa.

The sudden appearance of all the phyla without any transitional forms is one of the chief reasons rendering a complete theory of evolution from one or a few original ancestors up to all the present forms difficult to hold on scientific grounds. The facts are clear. It is true that the known fossils of the early period are only a small sample of the organisms which actually existed. And the Pre-Cambrian and Cambrian Periods lasted for many millions of years. But fossil samples within the family level downwards to species are fairly representative and comprehensive. Thus it would seem, on statistical grounds alone, that some forms undoubtedly connecting some of the phyla should have been found in the hundred years or so during which intensive search has been

made for fossils. Some evolutionists have tried hard to overcome this great difficulty, but many of their arguments appear to be forced, or to beg the question. For example, G. G. Simpson¹ wrote that: 'As H. E. Wood has remarked, the argument from absence of transitional types boils down to the striking fact that such types are always lacking unless they have been found.' It is true enough that argument from a negative does not give a sure foundation for a constructive theory, but the onus of proof of a theory lies with its upholders who must take account of *all* negative and positive facts available.

Many explanations of the absence of connecting series between phyla have been given, but in general they seem to be based on what is called the 'imperfection of the fossil record', and on an argument that assumes all of these connecting links must have been soft-bodied and unsuitable for fossilization in the Pre-Cambrian Era where they could legitimately be expected to occur. The argument from the imperfection of the record is one which leads nowhere and gives no useful conclusion. The palaeontologist can always say that connecting links may be found in the future. But this argument is based on the assumption that the record is actually imperfect. It is true that it is imperfect in the sense that only an infinitesimally small fraction of all the individual organisms which have ever lived have been found as fossils, but this does not necessarily mean that representative samples of types of organisms have not been found. In point of fact several millions of fossils have been found and these include a large proportion of known genera and many extinct ones. A statistical analysis of known fossils on the basis of their type is badly needed. Some few attempts at such an analysis have been made. Dewar² gave some counts of genera of fossils which had been found up to 1942. Among mammals he found that where the number of living genera in a family is very small (1.5) one hundred per cent of them have been found as fossils. But where the number of living genera in a family is not small the percentage of them found as fossils varies, but is on the whole high and generally well over fifty per cent. Of all the genera of living land mammals in Europe, one hundred per cent have been found as fossils; while for Asia the figure is seventy-two per cent, for Africa fifty-four per cent, for North America ninety-four per cent, for South

¹ 1950, p. 233.

² 1932 and 1942.

America seventy-two per cent and for Australia forty-six per cent. Figures such as these, which are concerned only with animals which leave fossilized hard parts of their bodies, tell us nothing about soft-bodied creatures, but at least they do suggest that the fossil record may not be as imperfect as it is commonly supposed to be. Such figures are very useful when considering the evolution of the higher animals among which large gaps also occur. The results of Dewar's analysis emphasize that it is always the critical connecting links between groups which rarely seem to fossilize, or which lived in regions now inaccessible to modern investigators.¹ In spite of the enormous numbers of what are called the mammal-like reptiles of the Karroo formation, Broom was really unable to say which forms may have been the possible ancestors of the vertebrates.

The argument that the connecting links may have been soft-bodied undoubtedly has some bearing on the problem, but again it is negative, and neither affirms nor denies evolution. But, as the early phyla seem to appear 'suddenly' in the rocks always as fully formed members of their particular phylum, some links should have appeared in the earlier Pre-Cambrian rocks many of which were suitable for fossils. One may reasonably conclude that there is no absolute proof from palaeontology of connections between the phyla and either (a) that the connecting links have not been found because there were never any to find (which is unlikely), or (b) that for some unknown reason, or reasons, conditions were not favourable to fossilization over many millions of years, but that on a general view a hypothesis of evolution of the phyla may be stated as a working principle awaiting a more rigid proof from palaeontology.

b. *Adaptive radiations*

A significant feature of palaeontology is that, excluding the phyla, as we proceed to study the fossils from classes to orders, families and genera, the general pattern of evolution becomes more and more evident and decipherable in spite of gaps, and moreover, in respect of these lower categories, the evidence of resemblance from palaeontology may be united with the evidence

¹ A recent excellent review on these topics has appeared since these pages were written; see Simpson (1960), which gives a partial answer to some of the doubtful points.

from comparative anatomy and morphology, making the demonstration of true relationship more certain. Within the genus and family some very excellent evolutionary series of fossils have been found, and later on we will give one or two examples of these in some detail. At present, on the assumption that evolution has occurred, all we wish to do is to indicate some general trends and patterns which palaeontologists have found by studying fossil members of classes and sub-classes. There are no absolutely complete fossil series within a class in which the orders, families and genera are connected piece by piece as it were, but the general trends are often quite clear. The vertebrate classes provide the best examples because vertebrate animals possess a hard skeleton and many of their fossil forms have been found. A general survey shows that, starting with the most primitive ones, great outbursts of evolution occurred within a class producing forms which diverged from a common stock and which were probably peculiarly adapted to particular environments. Such outbursts are spoken of as *adaptive radiations*.

The term adaptive radiation was first used by H. F. Osborn¹ to express the history of animals in a general way. The vertebrates may be taken as an example. Since their first appearance the various groups of these animals have each in turn increased in numbers and variety, probably due to favourable environments, which were then exploited to the full, and, at the same time, the dominant group split up into many types of families and genera. Simultaneously organisms developed which were to produce later radiations as the environment changed in the course of millions of years. Thus it becomes possible to speak of the age of invertebrates, of fishes, of amphibians, of reptiles, or of mammals ending with the age of man. An important point to notice is that these radiations of the various groups occurred in the order just given which is also the order in which on morphological grounds we would expect them to have evolved. The order of their succession in the rocks is, broadly speaking, the same as the order of their increase in complexity in form and structure. Osborn and all subsequent writers emphasized that the key word in the phrase 'adaptive radiation' is the word *adaptive*. The adaptations are generally progressive and enable the organisms concerned to spread into other environments, thus increasing their range and

¹ 1925.

possibilities for change. The evolution of all forms in such radiations is looked upon as the response of the organisms to their surroundings, and this is supported by the evidence. As these changed and favourable types were enabled to branch out, they in their turn became dominant. The evolving organisms show a response to the environment in several ways; for example, all the major characters of the organism may change, or the change may only affect certain parts of the animal's body, such as bones which become altered in different proportions. Sometimes the changes seem to be gradual ones, at other times they seem to appear more or less suddenly. Osborn¹ considered that he had discovered a new principle of biomechanical evolution which he called *aristogenesis*, through a study of adaptive radiations in fossil series.

Aristogenesis depends on changes in the germ-plasm of organisms, and it is a type of 'creative' evolution. Adaptive radiations are expressed in two chief ways by means of allometrons and aristogenes. The former express an independent, or particulate, adaptive radiation which is seen in the modification of existing organs in animals. Examples of allometric changes are seen in many fossil and living animals as changes of the proportionate size of limb bones, tails, heads, etc. An increase of one part of an organism may be correlated with a corresponding decrease in another part which revealed something of the habits of the animals concerned. Such changes are brought about by physical and living environments, habits and predispositions of the animals. Thus in general allometric changes do not follow any set path or trend. On the other hand, aristogenes are adaptive characters which arise directly from the germ-plasm and begin new evolutionary trends. Examples are seen in the evolution of teeth of various mammals. In some fossil series new elements (or production of new aristogenes), such as a new conical element on a grinding tooth, can be seen to have arisen spontaneously. For example, the grinding tooth of the mastodon, *Mastitherium Andrewsii*, found in the Eocene Period, started with seven conical elements (or aristogenes); in the Oligocene Period *Phiomia Osborni* had ten conical elements; while in the Lower Miocene *Trilophodon Cooperi* had twenty and the Upper Miocene *Trilophodon macrognathus* possessed thirty-seven elements.² Thus, in the period from

¹ Various papers, 1931 a. and b., 1933, 1934; and see Fothergill, 1932, pp. 274-280.
² Osborn, 1933, p. 701, and 1934, p. 244.

Eocene to Miocene thirty new aristogenes had arisen in the grinding teeth of these mastodons.

c. *Orthogenesis*

Osborn's idea of aristogenesis is essentially orthogenetic and this brings us to the second pattern of evolution said to be revealed by palaeontology. G. L. Jepsen¹ pointed out that the word 'orthogenesis' was first used as a biological term by Haeckel in 1893. But before then the principle behind all of the orthogenetic theories was formulated in a purely intellectual theory by Carl von Nägeli in 1864. Nägeli considered that evolution consisted of a progression towards structural perfection brought about by indefinable internal urges and co-existent with this striving there was also a striving towards perfection of adaptation. Kotschinsky,² who was also an orthogeneticist, expressed this view as follows: 'In order to explain the origin of higher types out of lower it is necessary to assume a special tendency towards progress in the organism.' It is commonly stated that orthogenesis is a theory which attracts many palaeontologists, and it is true that these scientists have described many orthogenetic series of fossil forms. G. L. Jepsen,³ however, pointed out that orthogenesis as a theory has probably been accepted more by biologists than by palaeontologists, but, as a descriptive term for phylogenetic arrays of fossils, more by palaeontologists than by biologists. Thus the word has been used in different senses by different scientists. For a good account of its various meanings the reader may be referred to Jepsen above.

In ordinary use in biology and palaeontology the term refers to straight-line evolution. A type of organism evolves through the ages by means of changes which follow what seems to be a pre-destined pattern, much like the pattern of a carpet which becomes evident as it unrolls. Generally speaking, all advocates of orthogenesis as a theory of evolution imply that it shows the operation of law, and so the theory has been held to stand in opposition to Darwinism which was supposed to show the operation of 'pure chance'. The factual evidence for orthogenesis is furnished by evolutionary series shown in some families, as, for example, in the fossil records of the horses, camels, elephants, the titanotheres, the ammonites and so on. In earlier days Darwinism

¹ 1949.

² 1893, p. 273.

³ 1949.

was often held to be unable to explain the determinate development of evolutionary series of organisms along what seemed to be fixed lines which were not always adaptive, or to explain the incipient stages of incipient organs before they had reached the useful stage, or to explain the over-development of certain organs or parts of animals, such as the very elaborate plumage of some birds, or the huge size of some of the prehistoric reptiles. Orthogenesis, or evolution along predetermined lines, could give an explanation of such difficulties as these. An account of some orthogenetic series will be given later.

The modern position seems to be that orthogenesis, as a theory of evolutionary causation, is gradually being abandoned in favour of selection, because, from the biologist's point of view, orthogenesis has teleological implications which he is not prepared to accept, and because it has been erroneously supposed that orthogenesis runs counter to selection. Whether there is an internal urge, or a directed process at work, or not, it is obvious that if major changes in an organism are not adaptive it will not live. Adaptation in this sense is merely another name for life. In 1913 L. Plate introduced the term *orthoselection* which also gives an explanation of some orthogenetic series in animals. By orthoselection is meant that if an adaptive trend exists selection will lead to improved adaptation providing the environment remains relatively stable and the trend continues. As Romer¹ wrote: 'Under such conditions any deviation from the "normal line" would be negative as to survival value, and would tend to be eliminated: the potential branches of the "tree" would tend to be pruned by selection before they became marked enough to become apparent in the fossil record.'

There does not seem to be any direct evidence for orthoselection, but the conception is a very useful one and in fact J. S. Huxley² wondered why it had not come into more general use. Nevertheless, the idea of orthoselection presupposes the existence of a trend in an evolutionary series, and so this still needs an explanation short of the assumption of the effects of a series of unidirectional and progressive mutations spread over many millions of years.

¹ 1949, p. 107.

² 1942, p. 500.

d. Examples of fossil radiations and series

In palaeontology it is often much more difficult to trace the evolution of individual species than to trace the probable line of evolution of larger groups. D. M. S. Watson¹ discussed this matter and pointed out that the reason for it is the small number of differences between closely related species and the smallness of the actual variations themselves, while among larger groups such as families, some common larger characteristics of the organisms tend to be persistent while numerous other smaller characteristics change as evolution proceeds. The process in order to establish an evolutionary series thus becomes easier in larger groups if plenty of material is available. As Watson wrote:¹

It will be appreciated that the doubts presented by series [of fossils] purporting to show specific changes of character arise from the fact that the process of selection of the materials which compose the series necessarily depends on small qualities, and generally on very few of such. If we can avoid these difficulties by dealing with groups which at the particular horizons concerned are sharply marked off from all others, and use the whole of the available material, we are in a much stronger position. Thus it is possible to consider the relatively large structural changes which are common to all members of a relatively large group, a family or sub-family, over a prolonged period by making use of everything wherever it may be found, in a continent or over the world, as the basis of our series.

In these words Watson outlined the working method of the palaeontologist who seeks to build up an evolutionary series. What the palaeontologist really does with the fossils is to use them in order to build up a classification in a similar way to the systematist who constructs a classification of living forms. In both cases the classification is based upon similarity of form and structure among the organisms classified. Given enough specimens neither the systematist nor the palaeontologist has any great difficulty in grouping together members of, say, the Compositae among living plants, or the Equidae among fossil and living animals. Both the palaeontologist and the systematist tacitly assume that their classifications show, or indicate, the closeness or otherwise of genetic relationships and the lines of

¹ 1949, p. 47.

descent among the organisms they classify, i.e., they attempt to make their classifications natural and to show the trend of evolution of the organisms concerned. It is open to anyone to doubt the reliability of the evolutionary inference which is made from the series which have been established in this way, but then the similarity of structure between the organisms concerned would require some other explanation. Beyond assuming special creation of different forms of creatures as they are, no other explanation has been put forward, or indeed seems possible. Generally speaking, it is clear that resemblances between members of species will be closer than resemblances between members of genera and closer between genera than between families, and so on. The result of this fact is that related genera are farther apart in a genetic sense than related species, families than genera, orders than families, etc. And while it is true that in practice it is easier to build up a family series of evolutionary relationships compared with a species relationship, when we go above the family as a unit of classification the divergences between organisms become very much greater and the point is reached when on fossil evidence alone the connections between higher groups is suggestive only and not proved. It is at this point that interpretation of the fossil evidence may vary among different palaeontologists. Also, one's reaction to suggestive evidence of this kind will vary according to whether one is convinced that the whole picture of the history of organisms is an evolutionary one or not. Thus D. Dewar may legitimately argue that because the fossil record does not show an unmistakable series of forms connecting order with order, class with class, etc., then the conclusion is that these categories have not evolved one from the other. But such people tend to overlook the other lines of evidence of evolution which together with the evidence from palaeontology unmistakably point to the existence of an evolutionary process in nature which is being slowly but surely worked out in greater and greater detail. For an excellent discussion on these lines, *pro et contra* the two views, the reader may be referred to *Is Evolution Proved?*, a debate by D. Dewar and H. S. Shelton. Palaeontology is the only method which the naturalist possesses of discovering the connections between extinct forms of organisms and in attempting to do so he uses the well-tried morphological criteria which the anatomist and morphologist have used so well on living forms and the validity

of which is experimentally demonstrated in some cases by genetics.

By way of illustration we may now give a few examples of trends and radiations as seen among the fossils.¹

c. *Evolution of Micraster*

For our first example we will give an account of a beautiful series in which species evolution may be traced. In 1899 A. W. Rowe worked out the evolutionary history and species distribution of the members of the genus *Micraster* from a geological zonal point of view. It is well known that individual species tend to die out and be replaced by other species of a similar kind. If these changing species occur in successive geological beds, or strata, then, providing sufficient numbers of specimens have been examined, an evolutionary series is presented. Rowe collected two thousand specimens of *Micraster* from different and accurately determined zones in the English Chalk Beds. The English (and Continental) Chalk Beds are very uniform formations consisting of nearly pure chalk. This chalk was originally formed on the muddy bottom of a fairly deep sea floor. *Micraster* was a sea-urchin which lived on, and in, this Cretaceous mud and its fossil remains are found abundantly in the chalk but in different concentrations at different levels. It is in fact one of the commonest fossils of the Chalk Beds.

Micraster is now extinct and it is a genus of the class Echinoidea, or sea-urchins. All of these echinoids were characterized by their body which was enclosed in a shell or *test* made up of many calcareous plates connected together. The sea-urchin which is so commonly found on our sea-shores is a good example. The sea-urchins possess characteristic structures called *ambulacral vessels* consisting of a series of tubes which fill with water and expand, thus projecting out through holes in the test. They serve as respiratory organs and as 'feet' for moving about.

The species of the genus *Micraster* possess a heart-shaped and

¹ There are many examples of these trends, etc., in various text-books, but the reader may be referred to K. A. Zittel, 1915; H. W. Shimer, 1933; H. H. Swinnerton, 1947; H. F. Osborn, 1923; R. S. Lull, 1934; A. S. Romer, 1933; T. S. Westoll, 1938; G. G. Simpson, 1936, for animals, and for plants to D. H. Scott, 1920; J. Walton, 1940; A. C. Seward, 1933; C. A. Arnold, 1947. For criticism of the fossil record the reader may be referred to Dewar, 1933, 1938, etc., and Dewar and H. S. Shelton, 1947.

bilateral test as shown in Figure 6. They had five ambulacral zones which are described as being petaloid, or wide, and when looked at from the ventral surface they radiated out from a centre like the radii of a circle. The anterior ambulacrum differed from the others in being placed in a distinct groove. The interambulacral zones were very heavily ornamented and worked which renders recognition easy.¹

Rowe collected his specimens from as wide an area as possible and he was able to show that only a few species were actually involved in the Chalk Beds, but that many varieties existed. In spite of the presence of these varieties Rowe found that the

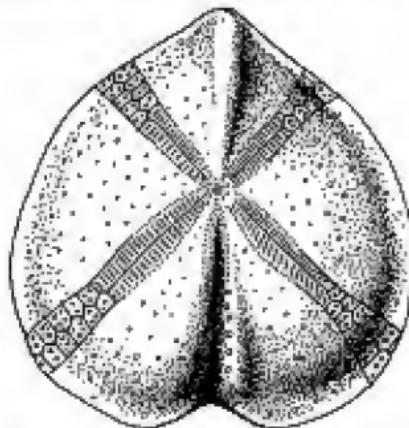


Fig. 6. Upper surface of *Micraster coronatus*. (After Nicholson and Lydekker, 1889.)

characters of the test fell into well-marked groupings in the different zones in which the sea-urchins were found. These character groupings were so distinct and definite that the zone could be determined by the presence of any one grouping provided sufficient numbers were examined. The genus *Micraster* was very prolific and plastic, which meant that examination of large numbers of samples had to be made before their relationships and evolution became evident. Discussing the delimitation of species from varieties Rowe said:

To arrive at any true appreciation of their value, both as to the validity of their claim to specific distinction and as to their usefulness

¹ See Nicholson and Lydekker, p. 389, Vol. 1.

as zonal guides, one must examine the facies of the genus in each horizon and then one cannot fail to be impressed by the fact that passage-forms are the rule and that sharply-defined and typical species are the exception. It is the horizon, and not the species, which rules the issue; the species are but culminating points of certain dominant horizontal characters.¹

In a zoological sense this means that the important zoological features are picked out in the species as shown by the test, while minor variations, or 'the passage-forms', show the connections between the species. Rowe concentrated on seventeen major features of the test, such as shape, size, mouth, ambulacra, etc., and was able to show that from the lowest zone to the highest there was an unbroken continuity in the evolution of the test of *Micraster*. Starting from the lowest zone and going up to the highest zone the test became progressively more elaborated by addition of new special features. The transition between all forms of *Micraster* was perfect and applied not only to the general features of the test but also to its minutest details.

Altogether in this evolutionary series only four species, or groups comprising all the group varieties, were involved. The first group is *Micraster cor-boris* which is practically the only one in the first or lowest zone of the chalk. *M. cor-boris* extended into the second zone and died out. The second group is *M. Leskei* which began in the lowest zone, but only one or two scattered specimens of it were found; it extended to the second zone and then died out. The third group is that of *M. praecursor* which appeared in the second zone, passed through the third zone to the lower part of the uppermost, or fourth, zone. The fourth group is that of *M. cor-anguinum anstorum* which was found in the fourth zone. The varieties, or passage-forms, in these groups indicated the sequence of changes necessary before one group became transformed into another one. An overall picture of the four zones in the chalk beds taken together is that they are divisible into a low zone characterized by *M. cor-boris* and an upper high zonal region characterized by *M. cor-anguinum anstorum*. *M. Leskei* and *M. praecursor* with their varieties occur in between. After the occurrence of *M. cor-anguinum* in the Cretaceous Period the genus died out in the English Chalk, but it persisted in other Continental regions right up to the Eocene Period.

¹ 1899, p. 497.

A peculiar feature about the evolution of the micrasters is that the sum total of changes is not really great considering they took place over a period of about sixty-five million years. The evolution of the micrasters was thus extremely slow. The changes that took place do not seem to have been of any particular adaptive value; the conditions under which they all lived must have been fairly uniform and unfortunately their evolution tells us nothing about the cause of the changes that took place in them over the years. Why should, for example, *M. precursor* have taken the place of *M. cor-boris*? Perhaps the scale of such a series as this is too small to give the answer.

f. Evolution or adaptive radiation of fishes

We may now briefly examine the evolution of the earliest fishes and fish-like forms which are, of course, the earliest vertebrates. The earliest undoubted vertebrates are the ostracoderms (or armoured fishes) and these appear in the Silurian rocks of about 350 million years ago. Many complete fossils of these forms have been found; they had a typical fish-like body, a tail and a backbone. They possessed a really complex internal and external structure as Stensio¹ showed. Because of their complexity it is generally assumed that they must have been in existence much earlier, and indeed some pieces of bone called *Astraspis* and *Eriptychius* have been identified by W. L. Bryant² from an Ordovician Formation. Other fossils are abundant in the Cambrian and the question arises, why have not more primitive fossil fishes been found in the rocks of this period? One explanation is that given by Romer and Grove³ and Romer,⁴ and other palaeontologists, on the basis that the earliest vertebrates must have been fresh-water forms and hence their fossil remains, except for odd ones washed down to the sea, would not be found in rocks laid down chiefly in the sea or in estuaries. Other palaeontologists, however, such as Gross,⁵ E. I. White⁶ and J. D. Robertson⁷ have adduced evidence indicating that the earliest forms of these animals were marine.

Older textbooks of palaeontology accepted the derivation of fishes from the lampreys and hags, i.e., from the Cyclostomata which were considered to be the most primitive vertebrates

¹ 1927 and 1931.
² 1931.

³ 1936.
⁴ 1938.

⁵ 1933.

⁶ 1946.
⁷ 1937.

because they did not possess jaws, had cartilage instead of bone and had no paired fins. The cyclostomes are eel-like in appearance and, as in higher vertebrates, as cartilage develops first in the embryos before bone is laid down, it was reasonable for the earlier workers to consider that the presence of cartilage was a primitive feature. The sharks and rays form an old group called the Chondrichthyes with living representatives. They are purely cartilaginous, hence primitive, but they possess jaws. The Chondrichthyes were considered to be derived from the cyclostomes and from them later arose those forms with many modern representatives which possess both bone and jaws; these are the Osteichthyes. At that time, however, many Palaeozoic fishes were known which did not fall into this scheme, but detailed studies of them had not then been carried out. In 1927 Stensio published a monograph on some of these little-known Palaeozoic fishes which set the pace for future work and led to a reappraisal of the evolution of the fishes when it became realized that bone was not necessarily an advanced development following on from the primitive cartilage. Readers who wish to pursue the evolution of fishes in greater detail may be referred to excellent accounts by Romer,¹ Swinnerton,² Westoll³ and several essays in Westoll;⁴ only an outline will be given here.

Fish and fish-like creatures, extinct and living, are most simply divided into two major groups: (a) the Agnatha, or jawless vertebrates and (b) the Gnathostomata, or movable jaw-mouthed vertebrates, which, of course, also includes all forms higher than the fishes such as amphibia, reptiles, etc.

As already mentioned the oldest undoubted vertebrate fossils are the Ostracoderms. In one order of these, the Osteostraci, the members were small, generally only a few inches to a foot long. Several types of them are known and they were all well armoured. In *Cephalaspis*, for example, a stiff solid bony shield covered the head region, while the rest of the body was protected by plates and scales. In side view the animal had a fish-like shape, and when looked at from the dorsal side it possessed a very characteristic shape due to the presence of the head shield. The eyes were situated close together on the dorsal part of the head, and the gills were underneath on the ventral side. Dorsal and ventral fins were present. *Cephalaspis* lay on the bottom of the sea with the eyes

¹ 1933, 1946.

² 1949.

³ 1949.

⁴ 1952.

directed upwards. The mouth was jawless, being merely a slit and there was a single nostril opening situated above and between the two dorsally-placed eyes. The head itself was also bony. The order Anaspida, including such forms as *Birkenia*, was contemporaneous with the cephalaspids and was similar to them but rather more advanced. The body of *Birkenia*, for example, was covered with an armour, the individual scales of

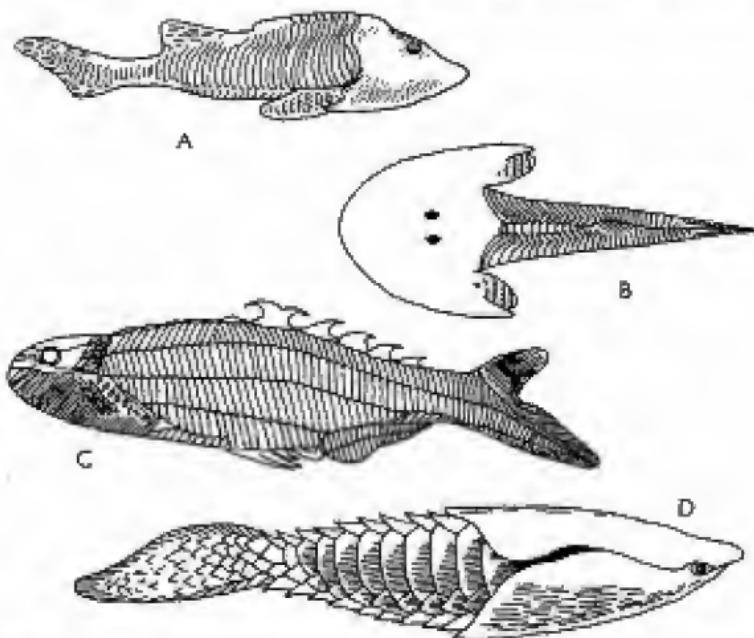


Fig. 7. Primitive fish. A - *Cephalaspis*, a late Silurian and Devonian Ostracoderm, side view; B - *Cephalaspis*, dorsal view; C - *Birkenia*, an anaspid from the Scottish Late Silurian; D - the heterostichous *Paraspis*. (A and C after Romer, 1933; B after Swinnerton, 1949 and D after Romer, 1946.)

which were arranged in neat rows along the body, while the head was enclosed in a very complicated arrangement of plates (Figure 7). There was also a series of spines along the dorsal crest of the back.

The forms mentioned above were very like the lampreys in general structure and even in such details as the presence of two semi-circular canals in the ear, but their forms differed greatly. The lampreys, however, do not possess bone, and as they are

parasitic or semi-parasitic, on other fish, it is now sometimes considered that they are probably derived from cephalaspid-like forms and are not ancestral to them.

In another order of ostracoderms, the Heterostraci, the species resembled Osteostraci by possessing a fish-like body enclosed in armour plates, but the head region was different. In the Heterostraci the head shield consisted of two large oval plates, the eyes were placed one on each side of the head, and there was no dorsal nostril opening. There were no jaws, but movable plates in the jaw region may have been present which suggests that the food of the animal may have been ground up to some extent, as in *Parapis* (see Figure 7).

The ostracoderms flourished in the Silurian and Devonian Periods, and they died out at the end of the latter Period. They are completely extinct now except for the agnathous lampreys and hags to which they are probably related. They do not seem to throw much light on the earlier evolutionary history of the vertebrates. Romer¹ pointed out that they show no connections with the zonellids or arachnids, although the presence of a gill system suggests their connection to lower Chordate types such as *Amphioxus* (or the tunicates). While the ostracoderms died out, the Gnathostomata, on the other hand, forged ahead and produced several groups in the succeeding geological periods.

The first group of jawed fishes is the Placodermi. These were also heavily armoured like the ostracoderms. The armour, however, was present in two sections connected by joints; one section covered the gill region, and the other the lower part of the body. Bony jaws were present; the eyes were placed laterally on the normal fish-shaped body, and fins were present. The jaws were rather peculiar, and it seems likely that the upper part of the head moved while the lower jaw remained stationary during feeding. These fishes were first found in the Late Silurian Period, and then they quickly increased in form and in number to become the dominant types in the Devonian Period. But after that they declined rapidly and died out in the Permian Period. The placoderms varied greatly in size from about a foot long (*Corcopterus*) to about thirty feet long (*Diplichthys*). Bone was present in them but their systematic position has not yet been settled. They may have been related to the ostracoderms but they had jaws.

¹ 1946.

Romer¹ considered they may belong to an extinct side branch of primitive gnathostome stock now represented by the sharks.

During the Devonian Period several other true fish groups arose which themselves split up into lesser divisions. As they advanced evolutionary changes took place in all parts of the body ultimately producing the present-day forms we know as sharks and rays (*Euselachii*), the lungfish (*Dipnoi*) and the 'ordinary' fish (*Holostei* and *Teloosteii*). There is no need to describe them in detail but the groups themselves may be mentioned.

The Chondrichthyes are the cartilaginous fishes known to us now as the sharks and rays, although the older more primitive ones possessed bone as well as scaly armour, like the ostracoderms. But these creatures were typical fish with movable jaws, fins, etc. This class is divided into the *Selachii*, the *Bradyodonti*, the *Euselachii* and the *Holocephali*. The first two orders originally appeared in the Devonian Period and were abundant in the Carboniferous Period. The *Selachii* then gradually dwindled until they died out in the Jurassic Period, while the *Bradyodonti* were extinct by the end of the Permian Period. Of the other two orders, the *Euselachii* were related to the *Selachii* and they first appeared in the Jurassic Period and extend up to the present day. The *Holocephali* may be related to the *Bradyodonti*, and they are first found in Triassic rocks also extending up to the present day.

The majority of present-day fishes, such as herrings, trout, etc., belong to the class known as *Osteichthyes*. The common characteristic of this class is the presence of bone in the internal skeleton and in the scales and plates which cover the body externally. One of the chief features of the earlier ones was that they possessed lungs as well as gills. Only the lungfish today possess lungs, and in the remaining fish the lungs have been transformed into the air-bladder. The *Osteichthyes* are usually subdivided into two sub-classes, first the *Crossopterygii*, or tassel-finned fish, and secondly, the *Actinopterygii*, or ray-finned fish. The *Crossopterygii* comprise the orders *Osteolepidoti*, in which the fins were rather like small paddles ringed with soft rays, the *Coelacanthini* and the *Dipnoi*. They first appeared in the Devonian Period, expanded rapidly into the Carboniferous and then gradually became extinct until at the present day only three genera of lungfish (*Dipnoi*) survive. Up to a few years ago it was

¹ 1933, p. 43.

also thought that the coelacanths had been extinct for some fifty million years until 1938 when some fishermen caught a peculiar fish in the sea off South Africa. Miss M. Courtenay-Latimer, Curator of the East London Museum, was informed and she in turn sent for J. L. B. Smith. The latter identified and described the fish as a coelacanth (see Plate 4). The discovery of this ancient type of fish makes very interesting and dramatic reading and the story is well told by J. L. B. Smith.¹ The Actinopterygii began with the Palaeoniscoidea in the Early Devonian Period. They were predaceous, and were common also in the Carboniferous seas, but they died out at the beginning of the Cretaceous Period. The Chondrostei were a small offshoot of the Palaeoniscoidea which began in the Jurassic Period. They possessed a nearly completely cartilaginous internal skeleton and a bony external skeleton. They survive at the present day as the sturgeons. As the palaeoniscids began to decline two groups arose which were to dominate the Mesozoic, Tertiary and Recent seas. These are the Holostei and the Teleostei which now form the vast majority of living fishes. The teleost fish represent the acme of development of the fish type which began with the primitive ostracoderms as revealed by the fossil record.

One interesting feature of the evolution of fish is shown in their body form which has always been adapted to the mode of life of the fish concerned. The normal fish body is shaped like a spindle flattened on each side. Such a shape is adapted for free movements in water. Another common shape, of course, is that of the flat-fish with its eyes on the back of its head and which lies on the bottom of the sea or river. Fish which float idly in the water tend to be laterally compressed while fish which move very quickly in the water tend to become long and pointed. These types have been described and illustrated by Swinnerton² and they are shown in Figure 8. The interesting feature is that these various adaptational forms are represented in all geological Eras.

Fishes, then, which represent the earliest true vertebrates, portray a wonderful series as they have appeared in the rocks. The series shows the process of evolution very plainly and at the same time the radiation of the various classes is also plainly discernible. First the most primitive group, the ostracoderms, appeared and radiated out in terms of numbers but not varying

¹ 1956 ² 1946.

much in form and then they died out. Similarly the placoderms, an advance on the previous type, developed quickly in both numbers and forms and then also died out. At the same time the major radiation of the whole group began when the majority of classes and orders appeared and dominated the Carboniferous seas. Some of these survived to the present day, but most forms became extinct and gave rise to another radiation in the Mesozoic

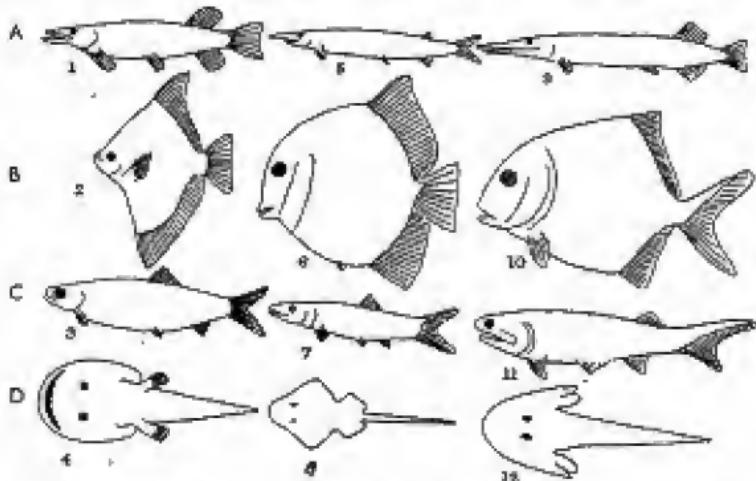


Fig. 3. Diagrams showing repetition of the same adaptational forms in fishes belonging to different geological Periods. *Horizontal columns:* A - arrow-shaped fish, B - deep-bodied fish, C - normal shaped fish, D - depressed fish. *Vertical columns:* Tertiary, Mesozoic and Palaeozoic Eras. 1 - *Esox* (pike); 2 - *Pomacanthus*; 3 - *Leptolepis*; 4 - *Chirodolus* (angler fish); 5 - *Aspidorhynchus*; 6 - *Pycnodus*; 7 - *Engelbatus*; 8 - *Squatina*; 9 - *Belonostomus*; 10 - *Platycephalus*; 11 - *Palaeonixus*; 12 - *Cephalaspis*. (From Swinnerton, 1949.)

Era from which most of our present fish are directly descended. While the main classes of fish remained distinct from the time of their first appearance in the rocks, they still showed many features of morphology which point to their evolution from common sources in earlier geological times, but of which no remains have been found. A diagram of the radiations and distribution in time of the fishes, adapted from Swinnerton,¹ is shown in Figure 9.

The Amphibia and all later vertebrates, including mammals, are thought to have evolved from crossopterygian fish such as the

¹ 1949.

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Rhipidista. The oldest orders of Amphibia were stegocephalian, i.e., they possessed a skull with a continuous bony covering. The oldest specimens of Amphibia found consist of a few bones from the Upper Devonian strata of Greenland. These are called *Icthyostega* and *Elpistostega*, and they were obviously well developed forms. As they were bony, it is unlikely that they

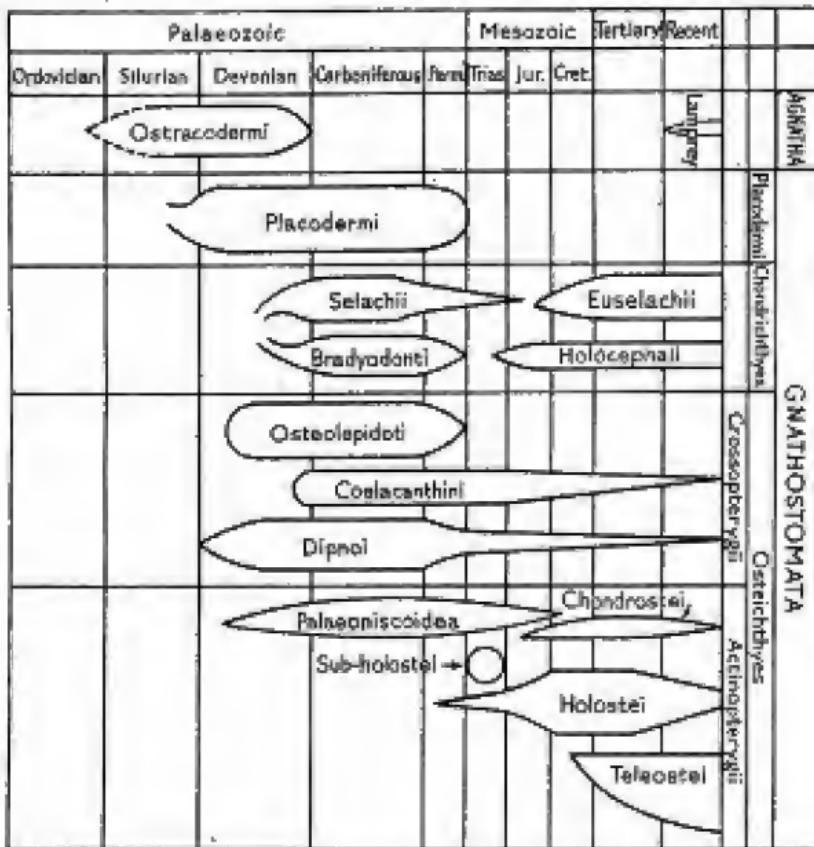


Fig. 9. Radiations and distribution in time of the chief fish groups. (From Swinnerton, 1949.)

could have originated from the cartilaginous fishes, which indeed at that time were only just themselves beginning to appear as far as the fossil record indicates. Thus only the Osteolepidoti, or Rhypidista, are left as possible forerunners of the Amphibia. Among the Rhypidista, the head bones of *Osteolepis* or *Eusthenopteron* seem to resemble the bones of the early Amphibia in

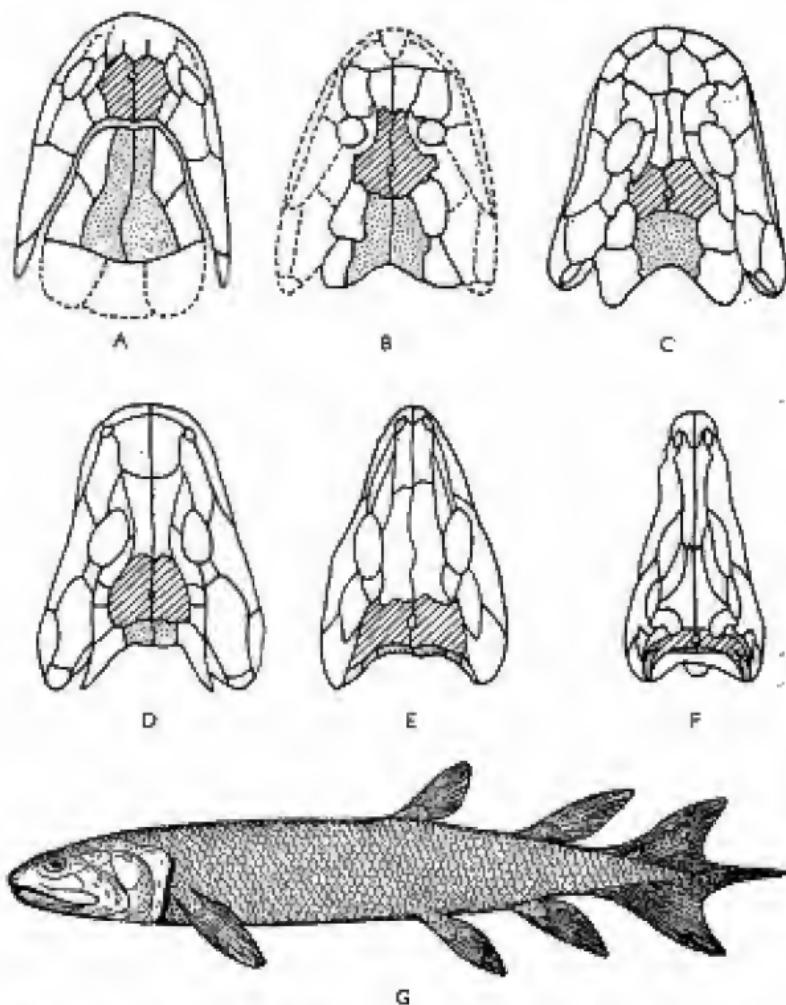


Fig. 10. A to F, a series of skulls in dorsal view showing changes of proportions from Crossopterygians to Permian reptiles. In A to F the posterior elements undergo steady reduction. The parietal bones are hatched and the post-parietals are stippled. A - Crossopterygian *Osteoptychus*; B - *Elpistostega* (early Upper Devonian, an advanced Crossopterygian or primitive amphibian); C - *Itaspidostega* (Late Devonian, a primitive amphibian); D - *Palaeosyntaxis* (a Carboniferous labyrinthodont); E - *Rauvius* (a cotylosaurian reptile); F - *Diplopleuron* (an early polycoleosaurian reptile); G - *Eusthenopercus*, a Rhipidistian fish believed to be the ancestor of land animals, actual length about 12 ins. (A to F after Romer, 1946; G from Smith, 1956.)

some ways (see Figure 10). These Rhipidista possessed fins and the Amphibia possess pentadactyl limbs, but there is little evidence showing any intermediate stages between a fin and an amphibian limb. There are, of course, many other differences between fishes and Amphibia (see also G. R. de Beer).¹

g. Other radiations and trends

The evolution of fishes furnishes a good example of a large-scale evolutionary series within a class, showing radiation rather than giving a detailed picture of step-by-step evolution. Within the class some good examples of smaller and more detailed serial changes are to be found, as, for instance, in the Diploï.² but the group as a whole shows well the broader changes that have taken place and it illustrates the point which Watson³ made that, given the material, the larger groups furnish good evidence of evolutionary trends. There are, of course, several other examples of this kind which we need only mention, such as the radiations among the reptiles which again is spread over many millions of years from before the Permian Period to the present time. Among these radiations many sub-groups, such as the dinosaurs, those huge prehistoric beasts, and their like, evolved and became extinct. As G. G. Simpson⁴ expressed it:

In the midst of all this radiation of the class Reptilia, the basic reptilian type came to be relatively rare and exceptional. Indeed, it nowhere survived in quite its original form. The expression of the Reptilia was not then simply a matter of the increasing abundance of one general type of animal. It involved, rather, the development of many and strikingly different types from an ancestry that had reached a new grade of organization. Some of these types converged towards, competed with, and occasionally quite replaced other animals that had earlier developed in radiation from more ancient grades of organization.

The great class of Mammalia, the mammals, also furnishes a striking example of large-scale radiations which we are in the midst of at the present day when it is usually considered that human beings, as the peak of evolution of the Primates, introduce a new factor into evolution by being capable of controlling the direction of evolution. We will, however, be dealing with the special case of the evolution of man in a later chapter.

¹ 1954, pp. 164-165.

² Westoll, 1949.

³ 1949 and see p. 10.

⁴ 1950.

Another kind of evolutionary series, which are also minor radiations and often take place at the family level, are those series often spoken of as showing orthogenesis, or straight-line evolution. Whether or not evolution in such a series is controlled by some 'inner urge', or by orthoselection, need not detain us now (we have already mentioned this point); the fact is that such series either show true orthogenesis or simulate it, although it is now known that orthogenetic series are not necessarily straight-line in the sense that no branching-off from the main line of evolution of the stock can take place. It seems that such orthogenetic series may break up into several lesser orthogenetic series. The important point for us is to note that series of this kind present very strong evidence for the occurrence of evolution. More or less continuous series of fossil types enable us to visualize evolution as a consistent process.

There are many examples of this type of evolution and we may mention the following: the Nassidae, a family of dog-wheas, the Cypraeidae, a family of Cowrie-shells, the Limnaeidae, a family of snails, the Halicoridae, a family of the Sirenia, the Anomia, a family of bivalves and the Nuculidae, another family of bivalves. For a further account of these series the reader may be referred to A. M. Davies¹ and also to D. Dewar² who considered that evolution has not been proved in these cases. Other, perhaps more familiar, examples are seen in the evolution of the horse, elephant, camel, rhinoceros, etc. For a general account of these cases the reader may be referred to Swinnerton,³ Osborn⁴ and Watson.⁵ We may here briefly consider the evolution of the horse family, or Equidae.

The evolution of the members of this family is well known and it presents one of the best examples which the palaeontologist possesses. There is a great literature on the subject and we need mention only W. D. Matthew,⁶ who was the great authority on the subject, and a most interesting account of modern and extinct horses given by G. G. Simpson⁷ where further references may also be found.

The story of the horse goes back to the beginning of the Eocene Period about seventy million years ago. It began with a small creature, about the size of a large dog, called *Eohippus* (or, more correctly, *Hyracotherium*), although there were different species

¹ 1937.
² 1946.

³ 1931 and 1938.
⁴ 1937.

⁵ 1949.

⁶ 1936.
⁷ 1946.

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which varied a good deal in size. At first it was thought that the horse fossils indeed gave a true example of straight-line evolution in the strict sense, starting with a primitive form and ending with

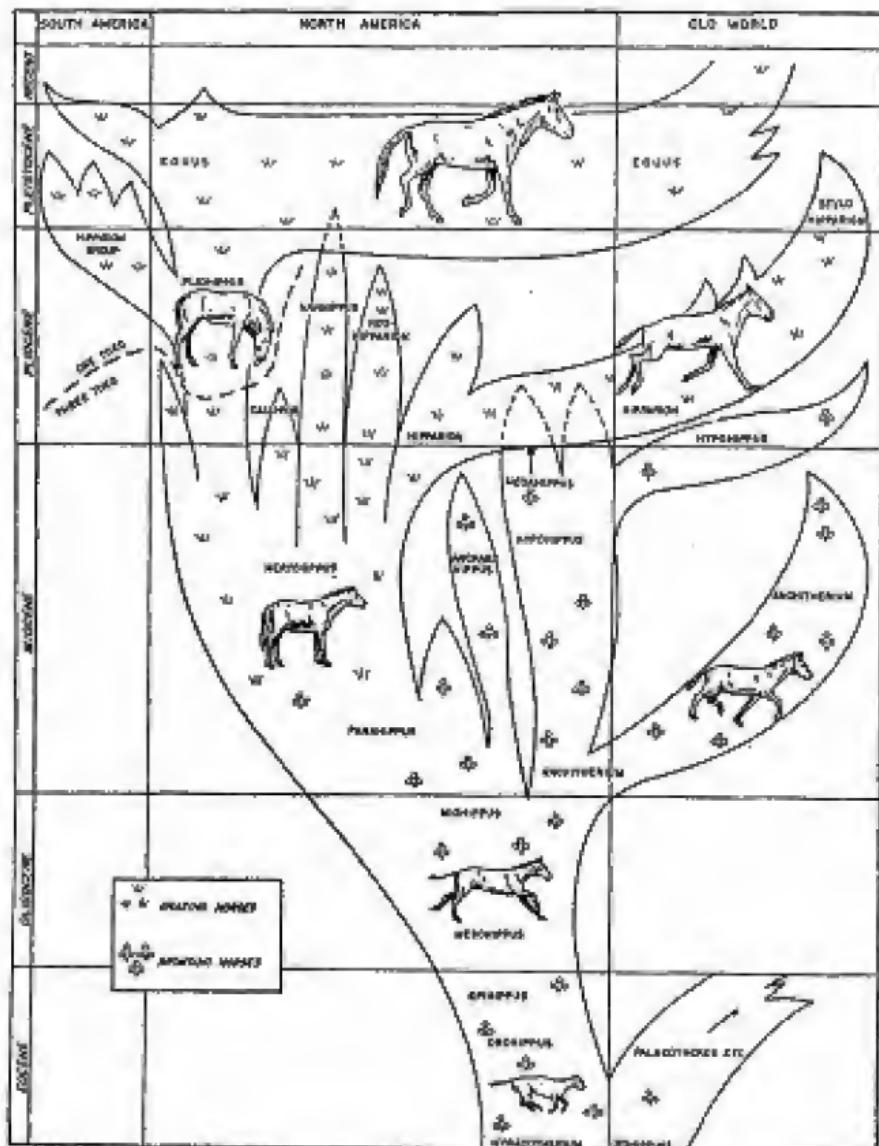


Fig. 11. The main lines of horse descent and relationships of the more important genera. The restorations are to scale. (From Simpson, 1931.)

Equus, the modern horse. But further study, and more numerous fossil finds, have shown instead that the extinct fossil horses comprise several sub-families and numerous genera (see Figure 11). But they have all probably arisen from *Eohippus* and throughout their long history they have changed in various directions to give the numerous genera. The direct ancestors of the horse as we know it today comprise, firstly, *Eohippus* in the lower Eocene Period, secondly, *Orahippus*, and then in the late Eocene Period, *Epiphippus*. In the next Oligocene Period *Mesohippus* and *Miohippus* made their appearance. These were followed by *Parahippus* and *Merychippus* in the Miocene Period and finally by *Pliohippus* in the Pliocene Period. All these became extinct and were succeeded by *Equus* in the Pliocene and Pleistocene Periods and this, of course, extends up to the present day.

In the early period, probably even before *Eohippus* had developed, the original horse stock branched off into the *Palaeotherium* or other types of ungulates. In the Miocene Period there were several branches, or radiations, leading to *Architherium* and to *Hippotherium*, while the *Equus* line went on to *Parahippus* and *Merychippus* in the Miocene when again several branches arose of which the chief one besides that leading to *Equus* was *Hipparium*. During this long period of evolution, the original types of *Eohippus*, which were relatively small, fast-moving creatures with four toes on each front and three on each back leg, changed in a large variety of ways. The number of toes became reduced to three with the weight of the body resting on the middle one, and further reduced to one, although some horses retained three toes, and so the familiar horse's hoof gradually developed. The bones of the legs also increased in overall lengths and in proportional lengths. Very characteristic and detailed slow changes also occurred in the teeth from the small teeth of *Eohippus*, which was a browsing animal, to the very large teeth of the modern horse, which are used for grinding food because the horse is a grazing animal. The skull and brain also showed a similar story of increase in size and complexity. Some of these changes are shown in Figures 12 and 13.

It is not known where the horse family first started geographically, but there is some evidence to show that North America was the original home of the family, and it spread from there, probably in several waves or invasions, to South America and also to the Old World, via the land connection which once

connected Alaska to Asia. The number of genera and types of horses and the number of their fossils indicates that the family must have been very numerous during the course of their

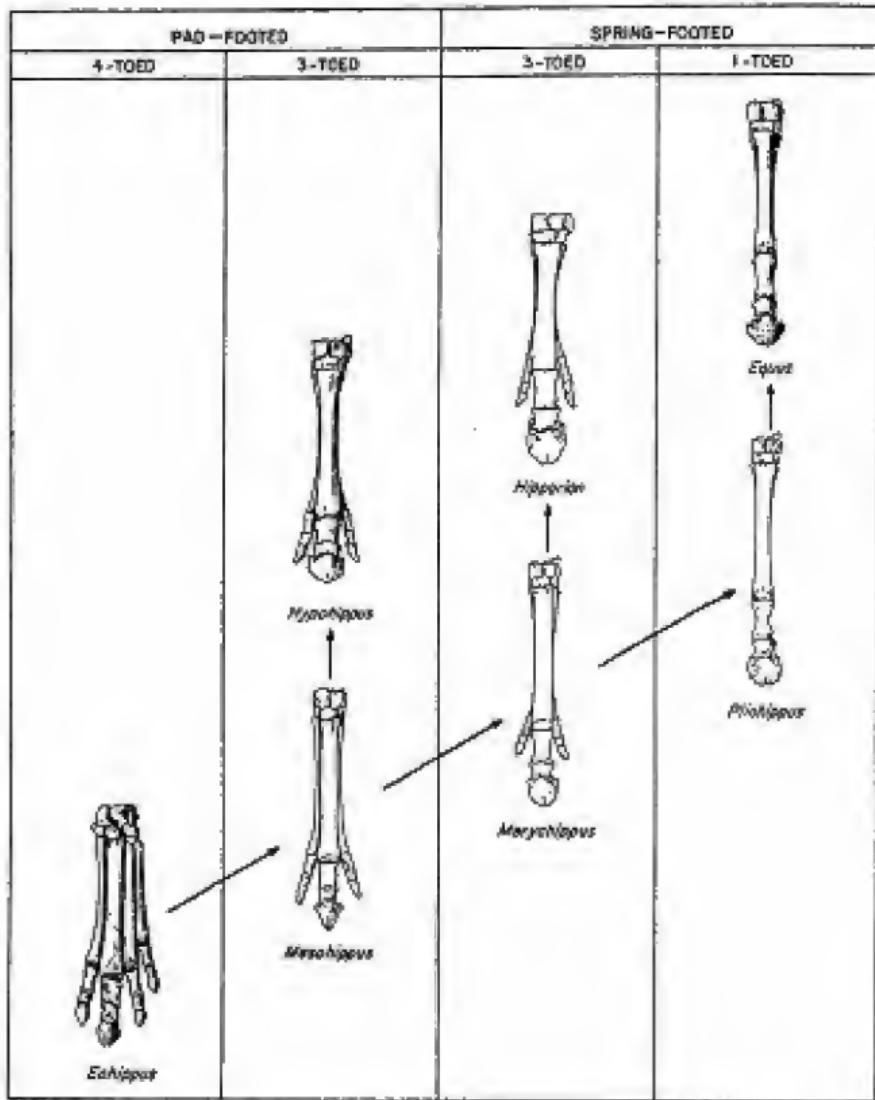


Fig. 12. Selected stages in the evolution of the forefoot of horses, oldest below. Each vertical column represents a distinctive mechanical type. Reduction of side toes seen as shift from type to type, that is horizontally. Not drawn to scale. (From Simpson, 1951.)

CLASSICAL EVIDENCE OF ORGANIC EVOLUTION

evolution. At the present time there are only about six distinct species of *Equus*, namely, true horses, zebras, asses and onagers. There are, of course, several varieties of each of these. The

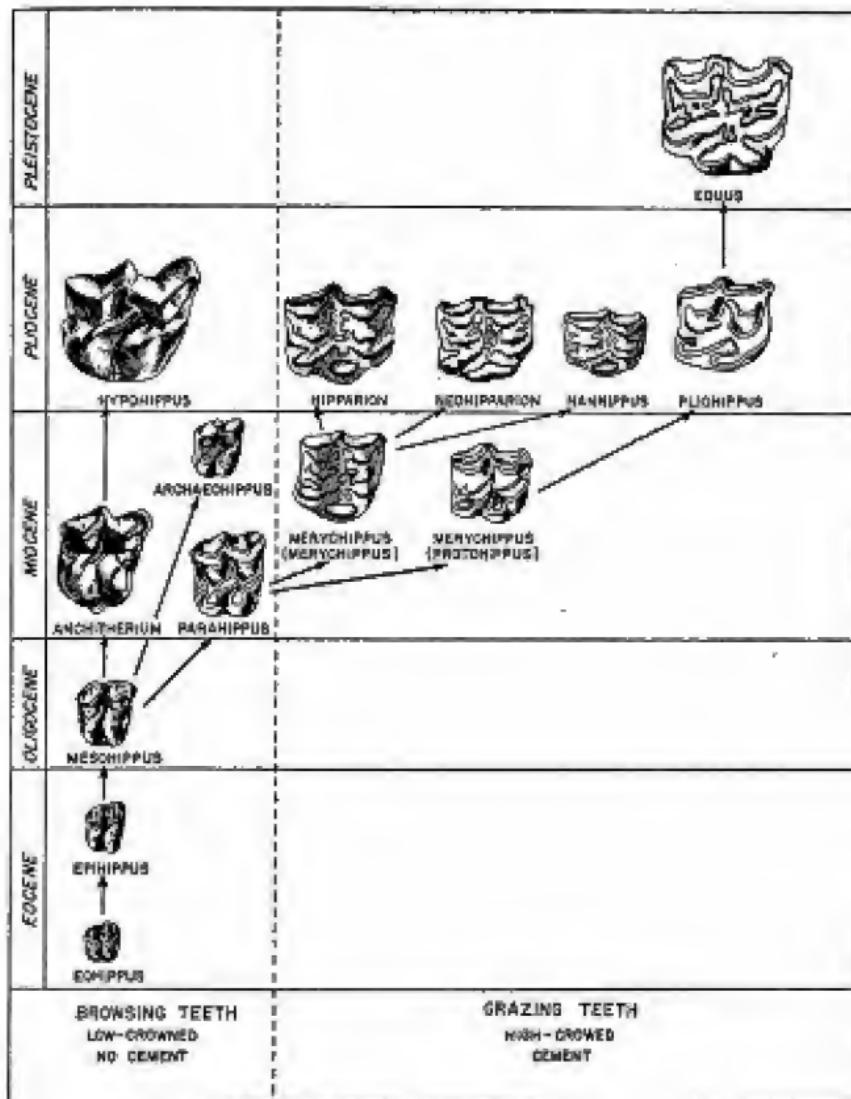


Fig. 25. Evolution of horse teeth showing changes in the grinding surfaces of right upper molars in various genera. (From Simpson, 1951.)

reason for the decline in numbers of genera and species of these animals is not known.

We have now given an outline account of the evidence of evolution in the palaeontological record. The outstanding fact about this record lies in its consistency. There are many evolutionary series of the general type which we have indicated in the preceding pages. These all point to and indicate an evolution within the family. There have been several larger radiations in animal series involving whole classes. Again, this indicates an evolution, but the matter here assumes a more speculative aspect because the jump from family to family within a class or order is larger than the jump from genus to genus within a family. In some cases there are reasonable indications of a possible line of descent from one family to another, but in other cases the relationship is shrouded in doubt. Very keen protagonists of evolution, those who have made up their minds about it beforehand, often tend to disdain such difficulties and breaks in the records, while, on the other hand, very keen anti-evolutionists, who have likewise made up their minds about the matter beforehand, tend to enlarge on them far too much as though the difficulties of evolutionary theory in this regard were really fatal to the theory. W. R. Thompson¹ was right to maintain that the discovery of intermediates between groups (and the lack of the same) does not necessarily commit us to any view about the origin of species, but this attitude is more correct when individual characters of organisms are considered. It is this question of the origin of species which necessarily remains the central problem of any well-balanced and methodologically correct theory of evolution, in spite of the fact that some evolutionary writers nowadays try to deny it. If, however, numbers of characters of the intermediate type are compared with numbers of characters in the organisms which the intermediate is supposed to link, then a new situation arises. Evolutionists have found that examination of many animals, fossil and living, shows that the morphological and anatomical features have often evolved by what G. R. de Beer² called *mosaic evolution*. As D. M. S. Watson³ had earlier noticed this characteristic of evolutionary development, de Beer proposed to call the phenomenon it represents *Watson's Rule*. By this term is meant that in evolution the whole body of the organism has not

¹ 1936.

² 1954, p. 163.

³ 1919.

evolved at once, instead individual characters all over the body have changed in their own way and in their own time. Hence in fully evolved types all of the characters would show their truly evolved condition distinct from those of another fully evolved type, while in intermediates a mixture of different kinds of characters would be shown. In other words, the intermediate would display a mosaic pattern of characters of different kinds, and depending on the extent of the mosaic pattern, the intermediate would be nearer to the original type or to the derived type. By means of this conception de Beer built up strong arguments for the evolution of Amphibia from fish, of reptile from Amphibia and of mammal from reptile. Nevertheless, the fact remains that all assumed transitional forms have always been controverted and agreement is not absolute. Thus, the scientific attitude would seem to be in some ways an unfashionable one of accepting the facts as they are and not proceeding beyond them unless we clearly indicate the nature and the bounds of our speculations.

It is hardly doubted nowadays that the celebrated *Archaeopteryx* (see Figure 14) is an intermediate type connecting the birds with the reptiles, but there are doubters and we may close this section by giving some information about it. It is well known that this bird-like organism possessed some reptilian features; for example, its skeleton is said to recall a reptilian form in many respects. *Archaeopteryx* possessed a jaw with teeth like those in some reptiles; it had a vertebral tail. On the other hand, it also possessed many undoubted bird features such as the presence of true and complicated feathers. *Archaeopteryx* and another form resembling it called *Archaeornis* were both found in Jurassic rocks. Romer¹ said: '*Archaeopteryx* and *Archaeornis* were already definitely birds but were still very close to the archosaurian reptiles in most of their structures and it is obvious that they were descended from that group.' On the other hand, D. Dewar² took exception to this claim and pointed out that any creature possessing feathers is an undoubted bird, and he asserted that many of the features of *Archaeopteryx* which are said to be reptilian are not in fact so. He considered that the skull is undoubtedly avian; that the absence of saddle-shaped articulations to the vertebrae is not necessarily a reptilian feature because some modern birds do not possess these

¹ 1933, p. 211. ² 1932.

articulations; and that the absence of pneumatic bones in *Archaeopteryx* does not mean that it is related to reptiles because pneumatic bones, in any case, are not confined to birds as a class for some reptiles possess them and some modern birds lack them, and so on. Again, while *Archaeopteryx* is said to be so bird-like



Fig. 14. Drawing of reconstruction of *Archaeopteryx lithographica* with enlarged section of tail. (After Romanes, 1893.)

and so reptile-like, there is no agreement concerning the group of reptiles from which it arose.¹

A recent re-examination of this creature, using ultra-violet illumination, was made by de Beer.² Under this light a number of new characters were discovered enabling a re-assessment of the

¹ Berg, 1926. ² 1934.

bird to be made. Thus de Beer found the following definitely reptilian features: simple brain with a small cerebellum, long tail of separate vertebrae, simple articulation of vertebrae, short sacrum, free metacarpels, free metatarsal, simple tib and gastralia in the body wall. While the true avian characters were as follows: feathers, arrangement of feathers, fused clavicles, pubes of the pelvic girdle directed backwards and the opposable hallux (big toe). In conjunction with de Beer's idea of mosaic evolution these new findings answer most of Dewar's objections. As de Beer¹ wrote: 'It [*Archaeopteryx*] is a mosaic in which some characters are perfectly reptilian and others no less perfectly avian. In its evolution from its reptilian ancestors, therefore, the modifications which it has undergone have affected some structures to produce their complete transformation while other structures have not yet been affected at all.' *Archaeopteryx* is thus a perfect example of Watson's Rule, and one could hardly wish for a better example of an animal linking two large groups together. On the whole, the important individual characters of *Archaeopteryx* are either bird-like or reptile-like, but they are not intermediate, although the creature itself as a whole may be said to be intermediate.

2. EVIDENCE FROM GEOGRAPHICAL DISTRIBUTION

The changes in animals and plants as they occur in successive strata of the rocks give us a picture of their distribution in time; and we have seen that the pattern of this time distribution is evolutionary. The spread of animals and plants throughout the world in past and present epochs, that is, their geographical distribution, also gives evidence of their evolution, otherwise the pattern of distribution remains inexplicable. The principle behind this type of evidence is simple, that, on the whole, due to normal reproductive mechanisms we expect to find like organisms grouped together geographically.

Some animals and plants are scattered all over the world, but many are found only in circumscribed regions. For example, *Urtica dioica*, the common stinging nettle, occurs in all the Northern Temperate Regions; it is ubiquitous. On the other hand, giraffes are found only in Africa. Climate, soil and other

¹ 1934, p. 162.

factors of the environment obviously play a large part in the distribution of plants and animals, but still there are many facts of distribution which cannot be explained solely by these ecological factors. Some organisms can overcome all, or nearly all, barriers and thus have a very wide distribution. Others, however, encounter various obstructions to their spread and thus these have a more confined, or smaller, distribution. Given the existence of barriers and reproduction, many of the problems of geographical distribution can be solved if it is assumed that evolution has occurred. Thus this type of evidence for evolution is indirect and assumes first what it wants to prove; nevertheless it is very convincing.

The evidence itself is cumulative and consists for the most part of a very large number of geographical facts, which, however, fall into only a few types. Geographical distribution connects to geology on the one hand and to geographical differentiation, or speciation, on the other. Geographical differentiation is due in large part to isolation and will be dealt with later under that heading. Full descriptions of geographical distribution have been given elsewhere, many of them by the older Darwinians,¹ to whom the reader is referred for further detail. Because of the similarity of the examples used it is necessary for us to give here only a few types of them to illustrate this line of evidence.

Very little evidence of evolution from geographical distribution is to be found among widely-ranging species such as man and many birds, except in a restricted sense. The evidence from geographical distribution is best seen among those species which have encountered highly effective barriers preventing their spread over a large geographical area. Thus oceanic and continental islands and other geographical regions which were once contiguous with mainlands, or larger land masses, give numberless examples. In all these cases seas or mountains have formed impassable barriers to many species which have not then extended their distribution, or if they have spread a little initially, characteristic changes in them have resulted.

Oceanic islands, such as the Azores, Bermudas, Galapagos and others, are all of volcanic origin and are isolated by deep seas and great distances from their nearest mainlands. In such islands,

¹ See A. R. Wallace, 1876, 1889; G. J. Romanes, 1893; C. Darwin, 1860; A. Heilprin, 1887; Lydekker, 1896.

which presumably have never been connected to any great land masses, the flora and fauna are usually very peculiar to them. For the most part the species on the islands are not exactly represented on the mainland, and *sive versa*. For example, when St. Helena was first discovered there was a complete absence of native mammals, land birds, reptiles and fresh-water fish. The isolation of the island prevented any of these animals reaching it. On the other hand it seems that beetles were carried to it on pieces of floating wood, and so the island contains about 130 species of beetles. But most of these belong to genera which are peculiar to the island and do not occur on the mainland. In other words those carried to the island have evolved along their own lines different from those on the mainland.

Charles Darwin first studied the fauna of the Galapagos Islands and he found that the animals inhabiting it were peculiar in many respects. The birds, in particular, showed unmistakable similarities to those on the nearest American mainland from which they could possibly have flown, but yet their distinctions were clear. Similarly, the Cape Verde Islands possess birds peculiar to them, but still showing unmistakable relationship to those of the nearest part of the African continent. Again, the fauna of the East Indies near Malaya show their own peculiarities, but they are all related to the species of the mainland. However, Celebes is the most isolated of these islands, separated from all the others by very deep seas, and there the most peculiar types are found, in some cases with no representatives on the mainland, or the nearest other islands. There are numberless similar examples of this type, and all find their explanation if we assume that those organisms which have reached these remote islands from the mainland have been able to evolve independently of continental influences and so have produced their own characteristic and peculiar kinds but still bearing the imprint of their more or less remote origin. On the other hand, if barriers to the spread of certain species have been too great then these species have been prevented from reaching the islands. Thus the presence and the absence of species on oceanic islands finds an explanation on an evolutionary basis.

The best examples of continental islands are probably Madagascar and New Zealand. These are considered to have been connected to the nearest mainlands in very remote times. This being so, we would expect the species common to both before the

connections broke to diverge along their own lines after the break occurred. Indeed the fauna of Madagascar is very different from that of Mozambique, the nearest mainland. Although separated long ago Madagascar possesses many of its own forms of mammals, birds and reptiles and many of these are very ancient and primitive. On the other hand, New Zealand possessed only about two mammals—a bat and a rat which were possibly introduced by man. It is considered that New Zealand was separated very early from the then mainland mass before the mammals had been formed evolutionarily, and this fact, which is geologically supported, gives the explanation of the lack of higher animals which are native to New Zealand. When this country was cut off, birds and reptiles had started to evolve and there are plenty of these present; but many of them are of peculiar types and some of them, such as the kiwi, or wingless bird, are found nowhere else except in New Zealand.

Plants also provide examples of this kind. In Australia and New Zealand, for instance, the flora is highly characteristic. In these large islands there is a very large variety of plants peculiar to them, but they belong to classes and orders represented on the mainland mass of South Asia. Again, in the Azores, most of the plant species are those which possess wind-blown seeds or fruits. These could originally have been blown there from Portugal which is 900 miles away. All, or nearly all, the plant species differ from those in Portugal and nearby places, but they belong to families and genera there. Finally, there is no need to multiply examples of this kind which find their best explanation in evolution.

Chapter V
Modern Evolutionary Theory

I. INTRODUCTION

THE continuity of life is the essential and outstanding fact underlying all evolutionary theories. This may seem a truism, but the fact is of relatively recent recognition. The theory of spontaneous generation was held from the earliest times and was only shown to be not proved by Pasteur and Tyndall about 1860-70. The origin of life, however, is a problem which does not concern the present organic evolutionist directly. He takes life for granted, as he is entitled to do, and he considers the progress of living forms after their initial origin. No doubt, if he advocates a theory of general cosmological evolution, then the origin of life enters into his scheme, and he may take up modern ideas which tend to resuscitate spontaneous generation in a more exact form, but all of these ideas are speculative and imaginative at the present time. The ideal is to connect animate with inanimate in a truly sequential scheme, and if this could be done, it would strengthen the claims of the organic evolutionist as to the veracity of his theory. There are no inherent difficulties, scientific, philosophical or theological, in the idea of a complete cosmological evolution of all things on the material phenomenological plane. Indeed, we may say there is good *a priori* possibility of the unity of inorganic and organic nature. The Cosmos shouts forth its multitude of secondary causes which are so clear and distinct as even to blind men to the existence of other causes. Hence, we take for granted that living things are only produced by living things as far as our experience goes, but still realizing that ultimately the origin of life is a problem which may have to be dealt with by the evolutionist of the future. Those readers who wish to pursue the question of the origin of life further may consult Fothergill¹ where modern references are also given.

It is this belief in the continuity of life by the evolutionist which

¹ 1938.

sets him against the theory of *Special Creationism*, because he can see no reason, or evidence, for the sudden creation of creatures when all his experience seems to show him an unmistakable progression of living forms on the earth. To a certain extent he is able to connect living forms one to the other; no doubt there are gaps in his schemes, but he considers he has reason to believe that, as his knowledge and his techniques grow and improve, his scheme of evolution will become more and more complete. A mere comparison of the state of evolutionary theory in Darwin's day with its state at the present time gives point to this belief of the evolutionist in his ability finally to solve outstanding problems of evolution, to his satisfaction at least. In a provocative book, bristling with controversial statements, G. G. Simpson,¹ a famous evolutionist, referring to the modern state of evolutionary theory, wrote: 'Within the realm of what is clearly knowable, the main problem seems to me and to many other investigators to be solved, but much still remains to be learned. Our knowledge of the material history of life is considerable, but it is only a tithe of what we should and can know.' Many people may probably consider this statement to be rather over-enthusiastic, but it does represent a common view among evolutionists.

It is necessary now to consider how this main problem has been 'solved', that is, we now give the modern genetic evidence for evolution. The subject is exceedingly vast, intricate and detailed; merely to give an outline of the subject would fill a large volume, as, for instance, J. S. Huxley's *Evolution: The Modern Synthesis*, which is recommended to the reader. Thus, of necessity, only some of the more general and important aspects of the subject can be given here, but we hope that they will be sufficient to enable the reader to form a more or less balanced judgment about evolution. Inevitably descriptions and accounts of the subject will be technical, involving terms and concepts perhaps unfamiliar to the general reader. To simplify the account given too much would merely stultify the object we have in view. For this reason some account of the basic ideas of genetics and cytology must first be given. Another reason for dealing with these subjects is that evolution now deals with things at the gene level, and even below it, and also, at the other extreme, at the population level which brings in specific genetical problems.

¹ 1950, p. 278.

It is perfectly clear that evolutionary changes could only occur through heredity. If parental characteristics, or changes, could not be transmitted through inheritance, there could be no evolution. The effective intermediaries between parents and offspring are the *gametes*, or sex cells. It is now firmly established that heredity (or a large part of it) is brought about by genes carried on the chromosomes—for our purpose we may ignore special cases of inheritance through the cytoplasm external to the chromosomes. Sexual reproduction, therefore, is the primary need in any evolving system of organisms (again, we may ignore cases which reproduce asexually).¹ As individual organisms transmit their characters to succeeding generations, any factors which assist, or increase, reproductive capacity have a great effect on evolutionary possibilities because then certain types of chromosomes and their contained genes are spread more and more through a population. Hence, a previous balance among hereditary units is upset, and a new balance is created, unless of course an equilibrium of some kind is established. But such an equilibrium would suspend evolutionary change at least for a time. Hence it is through genetics and the chromosomes that we must look for the fundamental evolutionary mechanism. That is why modern evolutionary theory is primarily genetical and based on the behaviour of the gene in inheritance.

In evolution we talk of the origin of species—this was the title of Charles Darwin's book, but it was really a misnomer. While all biologists would agree that the word 'species' has a meaning or meanings and that at least morphological species exist, few will venture to give a rigid definition of the word. We are aware that there are 'good' species in nature—for example, we can all tell an oak tree from a daisy—but differences are not always so large, and so we have some biologists who would consider one type to be a single species (lumpers) and others who would split it up into, say, a hundred or so separate species (splitters). As Hogben² said: 'Hence there is no one problem of the origin of species. There are many problems of the origins of species.' There may be systematic

¹ We are not asserting here that sexual reproduction is the only mechanism through which evolution or heredity or variation can be accomplished. Other processes such as parasexual recombination in fungi or transduction in *Pneumococcus* will play a part in lower organisms (see Pontecorvo, 1959) but we do not need to consider them here.

² 1940, p. 269.

or morphological species, elementary species, genetical species, physiological species and so on. In fact, each type of biologist may have his own particular idea of species to suit his own particular requirements and hence the word is often qualified adjectivally. This is the reason why it is so barren to argue about the meaning of species and to bemoan the confusion arising over the use of the word, at least in general accounts of biology. Such arguments rarely produce good results.

Hence, it is enough to say that nowadays in evolution and genetics the tendency is to regard the species as a *population* of like individuals which are largely interfertile; and in line with this conception of species, the emphasis in evolutionary studies has, in some respects, moved from the study of 'species', in the Darwinian or Linnaean sense, to the study of changes in populations. Individual members of a population are chiefly important only in so far as they are effective breeding members of the population. Sterile individuals have only a negative consequence in evolution (except at the human level). They withhold their hereditary substance from possible participation in the 'gene pool' of the population. They cannot exert a change in the population, but they may limit the extent of a change.

We mentioned the words 'gene pool'. This may be used in several senses, two of which are a particular and a general sense. A particular gene pool would refer to the totality of the genes available for inheritance in an individual, or it could even mean the totality of the genes in any one sexual organism which is actually participating in inheritance. The general gene pool could refer to the sum total of all the genes in all the individuals in a population of one type which are available in reproduction.

In a population, then, in which free breeding is taking place, it is easy to see that in every generation particular gene pools are constantly being intermingled, shifted about and sorted out, and while the net number of genes in the general pool may remain the same, innumerable new combinations are being tried out all the time. New combinations on a chemical interpretation of the gene imply new chemical reactions among the genes and hence change in the population. We may say that at this level such changes in a population would represent the evolutionary process in essence in the accepted sense. But, while the possible combinations of genes in quickly-changing gene pools are many, they

are not infinite. Change can be introduced in another way, and that is by gene mutation, in which a gene changes, not its relative position in the gene pool, but its very nature. A gene mutation is the production of something new.

2. FACTORS OF EVOLUTION

We have already mentioned that the four most important factors of evolution are *recombination*, *mutation*, *selection* and *isolation*. To these, subsidiary factors (which are really included in the primary ones) as, for instance, gene flow, genetic drift and others, may be added. It is our purpose now to consider these in turn and to show how they act in evolution. We will consider them only in outline with sufficient detail to give some indication of their nature and value in evolution.

A. Recombination

a. Cytology

Here we take the phenomenon of recombination in its widest sense involving any recombination of genetic units in the cell. Before attempting to give an explanation of the phenomenon, we give an outline of the structure of the cell and its behaviour in critical stages for genetic recombination. The phrase 'typical cell' is sometimes used in the literature, but this is a term of convenience only. There is no such thing as a typical cell—there are many types of cells, some young, some mature, some old, some differentiated or modified in various ways to produce the many different kinds of cells found in plants and animals. A body grows by increasing the number of its parts through division of its cells, at least in a multicellular organism, but in such organisms not all the cells in a body divide. Some are so much differentiated that they are unable to divide any more, and indeed some cells in adult organisms may even be dead, as in certain cells in the wood of trees. The cells which do divide, however, are generally young and it is this type which we may take for descriptive purposes.

Such a cell is bounded on the outside by a cell wall which is permeable to liquids (some cells have no wall), and inside is a substance which may be collectively called protoplasm. The protoplasm is alive in the truest sense, and it is very heterogeneous, consisting for the most part of two regions. These are the

cytoplasm and the nucleoplasm (nucleus). The cytoplasm is that part of the protoplasm which is outside the nucleoplasm. It is semipermeable, that is, it will only absorb, or take in, certain substances in solution and not others. It is the part where the metabolic activities of the cell in general occur. The cytoplasm appears to be clear, but contains granules of various kinds. These granules are generally referred to collectively as microcosms; some are exceedingly small; others are larger and differently shaped called mitochondria and there are other kinds. The nucleus is delimited from the cytoplasm by a nuclear membrane and contains nuclear sap, chromosomes, and one or more relatively large spherical bodies, or nucleoli.

We may now describe cell division which was discovered by Virchow in 1855. For a full account the reader may be referred to C. D. Darlington's *Recent Advances in Cytology*. In cell division the nucleus divides into two by a complicated and exact process called *mitosis*, and then the remainder of the cell divides into two so that each part contains one of the daughter nuclei. When not dividing the nucleus is often said to be 'resting', but, of course, it is not really inactive; it is in fact actively metabolizing all the time, but during this resting stage it often appears to be fairly homogeneous and clear. When a division, or mitosis, is about to take place the chromosomes make their appearance as long thin threads or *chromonemata* which are double in a longitudinal direction, that is, they have already split into two identical daughter halves in the preceding resting stage. These threads gradually thicken and shorten by coiling of the chromonemata separately until what is normally called the chromosome becomes evident. At this stage the two daughter halves of the chromosome are generally referred to as *chromatids*. The chromatid on this view is thus a later stage of the chromonema. At this stage the double chromosomes come together in one plane and the chromatids are seen to be separate from each other except at one definite point called the centromere. Suddenly the centromere splits into two with explosive force and then the daughter halves or chromatids of each original chromosome separate and move away from each other so that two daughter nuclei are produced each with the same number of daughter chromosomes as there were chromosomes in the parent nucleus. This process takes place in well-defined stages (called prophase, metaphase, anaphase and

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telophase) which we do not need to describe. Then these two daughter nuclei become separated by a new cell wall in plants, or by a constriction process in animals, producing in both cases two new daughter cells each identical to the parent cell unless an accident has occurred.

The process described above has been given in the simplest terms, but some complications will be mentioned below. What is a chromosome? And the answer is that no one really knows, but we do have certain knowledge about it. A chromosome is constant in shape and relative size, and the number of chromosomes is normally constant in each cell and in each species of organism. Each chromosome always reappears faithfully during cell division (excluding accidents). There is a good deal of evidence to show that it is in fact the bearer of the hereditary units, or genes, which pass on inheritance from parent to offspring. The exact form of division outlined above ensures that each body cell has a full complement of chromosomes containing all the genes.

The presence of two and later four¹ longitudinal chromatids was determined with the aid of the ordinary high-powered microscope, but modern methods utilizing the electron microscope have determined that there are in fact many more such threads in chromosomes. For further information the reader may consult Kaufman (1948), Manton (1950) and Kaufman and McDonald (1956). Multiple-stranded chromosomes were first demonstrated in the salivary gland chromosomes of *Drosophila* and other flies, but these are special cells in which division is considerably modified. Recently Kaufman and McDonald² have shown that there are sixty-four, or perhaps one hundred and twenty-eight, strands in the pro-phase chromosomes of the plant *Tradescantia*. The discovery of these strands raises many problems which will have to be considered in genetics and cytology regarding many fundamental cytogenetic phenomena, but these are problems for the future. Here we proceed on the basis that two or four strands, or chromatids, are present in the chromosome. The chromosome behaves as a unit and a problem is to determine how a multi-stranded chromosome can behave as a unit. The two-strand stage is typical of the division of the body or somatic cells, while the four-strand stage is typical of the division which gives rise to the sex cells, i.e., of *meiosis*.

¹ Nebel, 1952. ² 1956.

Modern work is also beginning to show the composition of the chromosome. Longitudinally, the chromosome under the action of certain stains or dyes is seen to be made up of alternate areas of coloured stainable parts, the *euchromatin*, and non-coloured parts, the *heterochromatin*. The heterochromatin varies in composition and stains differently with dyes, but the euchromatin stains positively with a specific stain called Feulgen's reagent which thus acts as a simple test for it. Euchromatin contains deoxyribonucleic acid (abbreviated to DNA) and the amount present in the chromosome can be correlated with the number of chromosomes. During the resting stage apparently it, or some of it, is diffused throughout the nucleus, but later it collects on to the chromosomes when division starts. Heterochromatin contains ribonucleic acid (abbreviated to RNA). If chromosomes are subjected to the action of the enzymes deoxyribonuclease and ribonuclease, which break down or dissolve the DNA and RNA respectively, a residue is left in the chromosome which consists of protein fibres.¹ These proteins are chiefly protoamines and histones which are characteristic of chromosomes. Specifically, the DNA in the chromosome is in the form of two long helically coiled intertwined chains which are joined together by hydrogen bonds. The joining is definitely determined by specific chemical bases so that purine bases in the DNA molecule are banded to pyrimidine bases, guanine bases to cytosine and adenine bases to thymine.²

The DNA is often nowadays regarded as the actual genic or hereditary substance, and the evidence for this rests on cytological, genetical and chemical grounds. Much of the work on this problem has been done in studies on bacteria and virus (phage) particles.³ A. E. Mirsky⁴ *et al.* when studying nuclei obtained from calf thymus found that the uptake of amino acids from a medium containing nuclei represented the synthesis of nuclear protein. Further, the build-up of amino acids into nuclear protein is controlled, to some extent, by the DNA present, because protein synthesis practically stops when DNA is removed from the nuclei and when restored the uptake of amino acid is resumed. This is an important finding if the DNA is considered

¹ See Kaufman, Gay, and McDonald, 1950, 1951; and Kaufman, McDonald and Gay, 1951.

² See Wilkins *et al.*, 1953; Franklin and Gosling, 1953; Watson and Crick, 1953. Purine, pyrimidine, etc., are complex nitrogenous bases.

³ Hotta, 1955.

⁴ 1956.

as the hereditary determinant, because it may then have some direct effect on that protein which is part of the basic chromosome structure. The genes in the chromosomes, and the chromosomes in the nucleus, are considered to act on the cytoplasm of the cell, controlling its metabolic activities as the need arises. The cytoplasm also shows a certain amount of activity in inheritance, but we do not need to consider this aspect. It is reasonable to hold, and in fact it is proved, that the co-operation of the nucleus and the cytoplasm in various chemical and physical activities results in all the metabolic and growth processes that are known, that is, in the life activities of the cell and hence of the whole organism. This important function of the chromosomes was realized as early as 1902 when Boveri deduced from embryological principles that 'Normal development is dependent upon a particular combination of chromosomes; and this can only mean that the individual chromosomes must possess different qualities.' We may note that it is a fallacy to introduce the 'nothing but' principle here and say that the cell and the organism is nothing but the sum total of the chemical, etc., activities going on in it. To prove this last point is a completely different matter, and it has never been done. We can see, however, how important it is for every living cell of a body to contain a full complement of the various determinants necessary for life's activities, and the perpetuation of this necessity is ensured by somatic cell division.¹

There is another very important type of nuclear division which takes place in all sexually reproducing organisms, and this type is called *meiosis*. In 1883 Weismann advanced his germ-plasm theory which became one of the landmarks in the study of heredity. The essence of the theory is that: (a) the body of the organism may be looked upon as two parts: first, the soma or body proper, and second, the germ-plasm, or reproductive part, which is distinct from the soma. Weismann went to extremes and separated these two parts more or less completely—which assertion even has its repercussions today among those who say that the body cannot affect the germ-plasm. (b) It is the germ-plasm only which transmits the characters of the parents to their progeny.² The sex cells are produced in this germ-plasm, and as in reproduction a male sex

¹ Good short accounts of modern knowledge of chromosome structure are given by W. G. Overend and A. R. Peacocke (1957) and in the *New Scientist* (1959).

² Weismann, 1892, see also p. 66.

cell unites with a female sex cell, i.e., when fertilization takes place, then the number of chromosomes in the product, or *zygote*, is doubled because each sex cell contributes an equal number of chromosomes. Obviously this doubling process cannot go on indefinitely at each fertilization otherwise the number of chromosomes would soon become astronomical, but the number of chromosomes remains constant from generation to generation. For *a priori* reasons there must be a compensating process to reduce the number of chromosomes, or to keep them constant. This process is called *meiosis*, and often it takes place during the formation of the gametes, although in many groups of organisms it takes place at other stages in the life-history.

Meiosis is fundamentally different to mitosis, both in its method and in its results. An outline description will now be given.

In the mother cell which is to undergo meiosis the chromosomes first appear as long single strings, or threads, which seem to be made up of blobs, or chromomeres, connected by fine threads. Incidentally, this chromomeric structure of the chromosomes is very well seen in the giant salivary gland chromosomes of some insects. These parts of the meiotic chromosomes correspond chemically to euchromatin and heterochromatin respectively. Almost as soon as they appear these threads begin to pair up chromomere by chromomere, so that one chromomere of one size and shape is paired with a corresponding chromomere of exactly the same size and shape. The chromosome threads first make contact at their ends, or at their centromeres, or at both at the same time. The pairing process is continuous and it runs along the threads like a closing zip-fastener. Sometimes the pairing is complete and sometimes it is only localized. Next, the paired threads coil round each other. It has been proved that, of the constituents of a single pair, one of the chromosomes comes from the ultimate female parent, and the other from the ultimate male parent. Thus the chromosomes in each pair are said to be homologous. Up to this stage there has been an attraction between the homologous chromosomes, but suddenly the attraction gives way to a repulsion, and as they repel each other, each chromosome is seen to be *double*, that is, each chromosome has split into two longitudinal halves, or chromatids, so that now in each association there are four daughter halves, or four chromatids. The repulsion is not complete because the chromo-

somes remain in contact at certain points. These points are called *chiasmata*. There is evidence to show that an exchange of parts between the homologous chromatids takes place at the chiasmata.

The uncoiling process continues, the chiasmata often move to the ends, or become terminalized, and at the same time the chromosomes shorten and thicken until they reach their maximum contraction, but they remain held together by the chiasmata and the centromeres. The pairs of chromosomes then assemble in one plane and the centromeres begin to repel one another so that in each case the complex of two chromosomes each made up of two chromatids separate from each other. In this way two nuclei are produced in the cell, each containing half the original number of chromosomes. Later, or in some cases almost immediately, each of these nuclei undergoes an ordinary mitosis when the chromatids now separate from each other. The process of meiosis thus consists first of a reductional division and then of an equational one and the net result is that four nuclei are produced each with half the original number of chromosomes.¹ In the general case each of these nuclei, or a near descendant of them, becomes a cell and ultimately a gamete. Darlington defined meiosis by its superficial phenomena as 'the occurrence of two divisions of the nucleus accompanied by one division of its chromosomes'.²

The importance of meiosis is obvious, first in reducing the number of chromosomes to the gametes and secondly by determining the *quality* of the hereditary material in the gametes. We have said that the homologous chromosomes of each pair come from the ultimate parents, and these chromosomes will be similar but not completely alike because of exchanges at the chiasmata. They will always differ in some respects and so let us represent them by AA¹, BB¹, CC¹, just to take three pairs. With their daughter halves or chromatids these would then be represented by AAA¹A¹, BBB¹B¹, CCC¹C¹. When these separate A always separates from A¹, B from B¹ and C from C¹, but the separation between the pairs, as pairs, is at random, for example we may get:

AA separating from A¹A¹

BB separating from B¹B¹

CC separating from C¹C¹ in that order.

¹ See page [157]. ² 1937.

Or—

AA separating from A¹A¹B¹B¹ separating from BBCC separating from C¹C¹ in that order and so on.

When the equational division takes place it is easy to see that gametes containing the following may be produced—ABC, AB¹C, AB¹C¹, ABC¹, A¹BC, A¹B¹C, ABC¹ and A¹B¹C¹. Given a large number of chromosomes, the possible combinations will rise quickly, and hence the quality of the gametes, that is, their genetic assortment, will vary also. This random genetic assortment, based on the chromosomes as the bearers of the genes, will be further increased if exchanges occur between the chromosome pairs, or if new genes arise.

Meiosis is, of course, subject to many complexities and irregularities according to the status of the organism in which it occurs. It is sufficient to mention here that in the ordinary plant or animal, for example, the association of two homologous chromosomes is called a *bivalent* which is the characteristic configuration in a diploid. But in triploids,¹ tetraploids, pentaploids, etc., that is associations of three, four, five, etc., chromosomes, there may be different numbers of *trivalents*, *tetravalents*, *pentavalents*, etc. While in *Oenothera* (the Evening Primrose) all, or nearly all, the chromosomes are joined in one huge association. Irregularities occur in polyploids² and even more in structural hybrids, because the association of chromosomes is not always complete and some may be left out, occurring simply as unpaired *univalents*, and sometimes much lagging behind occurs when the chromosomes separate, and some may be lost and thus not included in the daughter nuclei. To give a single example, Fothergill,³ examining a wild hybrid population between *Viola hirta*, a tetraploid with forty-eight chromosomes, and *V. tricolor*, a modified diploid with twenty-six chromosomes, found plants with chromosome numbers between twenty-six and fifty-three, while in meiosis many plants showed up to fifty per cent lagging chromosomes and associations varying from univalents up to sexivalents.

The mechanics of both mitosis and meiosis is thus fairly complex, but two forces are clearly at work—attraction and repulsion between chromosomes. In mitosis, the attraction and repulsion

¹ These words will be defined later.² 1938.

are between daughter chromatids, but in meiosis the attraction is between homologous chromosomes and their chromatids while repulsion is first between chromosomes and then between chromatids. The order of attraction and repulsion may vary so that in meiosis the equational division may come first and the reduction division second. The centromere seems to play a large part in the chromosome movements, but not very much is known about the physics of the processes involved. For detailed accounts, however, the reader may consult Darlington (1937), Waddington (1939) and Swanson (1958).

b. Genetics

It is well known that modern genetics springs from the pioneer work of Gregor Mendel, a Catholic priest and Abbot of an Augustinian monastery at Brünn in what is now Czechoslovakia. His experiments on garden peas still provide the simplest explanation of basic genetical principles and to preserve the continuity of our descriptions it is appropriate to summarize his work.

Mendel chose varieties of the garden pea (*Pisum sativum*) which showed pairs of contrasting characters¹ such as tall and dwarf plants, smooth and wrinkled seeds, green and yellow seeds, etc. For illustrative purposes we will use only the contrast between tall and dwarf plants, but whatever is said about this pair of characters applies also to all other pairs which Mendel used.

Mendel started with pure-breeding tall and pure-breeding dwarf plants. This means that when tall plants were bred they produced only tall plants and dwarf produced only dwarf plants. When these plants were crossed the first generation, or F_1 , plants were all tall. Mendel then conceived tallness as being dominant to dwarfness which was thus recessive. When the second generation obtained by crossing two F_1 hybrids was examined there were two kinds of plants in the proportion of three tall to one dwarf plant. Similar results were obtained with all the other pairs of characters Mendel used and so he concluded that some law, or laws, were in operation. To explain these results he postulated that in the parental gametes factors (now called genes) were present which gave various characters to the plants. He further postulated that when the gametes were forming those factors which came in from

¹ The word 'character' is invariably used in genetics meaning 'characteristic'.

one parent segregated or separated from those which came in from the other. This is called the *law of segregation of factors* and segregation occurs at random. When fertilization occurs these factors recombine at random; this is called the *law of recombination*. The process is easily illustrated by means of symbols.

If *T* represents tallness and *t* dwarfness, then, because tall and dwarf plants both received something for tallness or dwarfness respectively from each of their parents, a pure-breeding tall plant will be represented by *TT*, and a pure-breeding dwarf by *tt*. When these are crossed, *TT* \times *tt*,¹ the gametes will be *T* and *t* respectively, because the *Ts* and *ts* separate. When fertilization occurs the *F₁* will be *Tt*. When *Tt* is crossed with *Tt* the gametes will be *T* and *t* in equal numbers in each case and the combinations when fertilization occurs are obviously *TT*, *Tt*, *Tt*, and *tt*. As *T* represents tallness and this is dominant to dwarfness the result is three tall to one dwarf plant.

It is necessary now to introduce some technicalities. The plants represented by *TT* and *tt* breed true as far as tallness and dwarfness are respectively concerned; hence, in one case, all the gametes will be represented by *T*, and by *t* in the other. They are thus said to be *homozygous* for either tallness or dwarfness. The plant *Tt* is tall but produces two kinds of gametes, *T* and *t*, hence it is a *hybrid* and is said to be *heterozygous* for these factors. Again *TT* and *Tt* are both tall but obviously breed differently, and thus what an organism *looks like* is called its *phenotype*, while what *it is* in its germ-plasm is its *genotype*. *TT* and *Tt* are phenotypically alike but genotypically unlike, while *TT* and *tt* are both phenotypically and genotypically unlike.

We may now consider one other cross, called the backcross of the hybrid on to the recessive parent, i.e., *Tt* \times *tt*. When this is done the result is *1TT : 1tt*, or one tall to one dwarf plant. This is the one *1 : 1* ratio and it is a very important ratio in genetics because it indicates *one gene difference* between the organisms being crossed. In all cases of this kind the symbolism and postulates of Mendel agree with the experimental results and hence give an explanation of the principles involved. If we look closer at the *F₂* ratio of *3 : 1* we can extract some further information. This ratio is written down symbolically as *1TT : 2Tt : 1tt*; of these *TT* and *tt* are homozygous while *Tt* is heterozygous. The ratio

¹ The multiplication sign \times is used to indicate a crossing.

is then $1TT$ homozygote, $2Tt$ heterozygotes, and $1tt$ homozygote, that is, $1 : 2 : 1$. This ratio is the true, or *zygotic*, ratio and the $3 : 1$ ratio is a modification of this due to the dominance of one of the factors. If there were no dominance shown in this cross then the F_2 result would be 1 tall, 2 hybrids probably intermediate in size, and 1 dwarf plant. Many examples of this $1 : 2 : 1$ ratio are known and we need mention only one. There are two varieties of Four O'clocks (*Mirabilis jalapa*), red and white flowered. When red is crossed with the white-flowered variety the F_1 hybrid is pink and when the F_1 hybrids are crossed the F_2 result is 1 red : 2 pink : 1 white.

The $3 : 1$, or $1 : 2 : 1$, ratios are obtained when dealing with the inheritance of *one* pair of characters such as tall and dwarf. These ratios are said to be *monohybrid* ratios. When dealing with *two* pairs of inherited characters studied together, such as for example black and white coat colour, and smooth and rough coat texture in guinea pigs, a different ratio is obtained. This is called the *dihybrid* ratio. In guinea pigs black coat colour is dominant to white and rough texture is dominant to smooth. Taken separately these give a $3 : 1$ ratio in the F_2 generation. When a black-coloured, rough-haired animal is crossed with a white-coloured, smooth-haired animal the F_1 is black and rough, but the F_2 shows four classes of animals in a $9 : 3 : 3 : 1$ ratio as follows: 9, black rough; 3, black smooth; 3, white rough; 1, white smooth.

This ratio can be explained on exactly the same basis as the monohybrid one if it is assumed that the genes concerned operate or move independently, i.e., that they segregate and recombine separately.

c. Chromosome theory of heredity

Mendel's interpretation of his experiments has been amply verified, and most of the genetical experiments performed since can be explained satisfactorily on a Mendelian basis, or on some modification or extension of his principles. This is not to say that every experiment fits in with Mendelian assumptions. Lindgren, for example, claimed to have shown non-Mendelian inheritance in certain cases in yeasts. He has, of course, been criticised but not altogether refuted. There have also been serious critics of Mendelian conceptions and their criticisms are partially left unanswered because orthodox genetics is so successful. It should be

realized, however, that genetics deals with *differences* and the modern theory of heredity is an explanation of differences, and to a large extent the differences concerned are trivial or pathological. Mendelian factors, if such there are, pass in and out of crosses and their arrival can be predicted with accuracy. Granted the postulate of particulate inheritance, it seems to be in the nature of things that the movements of the particles will follow mathematical laws and the success of modern genetics stems from this fact.¹ Genetics gives us a satisfactory heredity of differences, but as someone has said, what we really want is an heredity of resemblances. The things that really count in organisms seem to remain more or less constant throughout most of biological history. To say that these vital parts do not change significantly because they are continually adaptive and hence continually selected seems to be begging the question and it certainly does not explain the matter, however ardently some people may claim that it does.

These are just opinions, however, and it remains a strong well-grounded assumption to postulate the occurrence in the germ-plasm (to use the old term) of unit factors controlling the expression of the visible characters of organisms, at least in so far as their inheritance can be investigated by means of differences. The germ-plasm is a definite thing, and hence these unit factors, or genes, should be definitely localized in some part of it. The behaviour of the chromosomes suggests that they are the bearers of the genes. It seems to have been Sutton in 1903 who first suggested this connection between genes and chromosomes because the latter as wholes also segregate at meiosis just like the genes and they recombine again when fertilization occurs. Thus the chromosomes behave just as Mendel's postulated genes do. This connection of the chromosomes and genes may be called the *chromosome theory of heredity*, but it is primarily a genetical, and not a cytological theory. The chromosome theory extends Mendelian principles and develops them logically due, to a large extent, to the discovery of linkage and crossing-over. Without it there would be no modern genetics and no modern interpretation of evolution.

The evidence for the chromosome theory of heredity is vast and is not confined to any group of plants or animals. In fact, it extends even to the bacteria, viruses and the phages, indeed it may

¹ See footnote 1 on page 170.

be from these microscopic organisms that new light will be shed on the mechanism of heredity, leading to a revision of some basic genetical concepts. To illustrate the theory we will choose simple examples from the well-known fruit fly, *Drosophila melanogaster*. This insect is very convenient for this purpose because it is easy to breed and produces a new generation about once a fortnight.

When the *Drosophila* work was first started it was soon discovered that its inherited characters fell into four groups, and the members of any one group were *normally* inherited together. It was also found that each cell of the fly possessed four pairs of chromosomes. This suggested that each group of characters could be identified with one pair of chromosomes. One of these pairs of chromosomes was found to be very small, so also there was a very small group of characters. The remaining three groups of characters and of chromosomes were approximately equal in size. The phenomenon whereby genes inherited as a group are considered to be carried on particular chromosomes is called *linkage*, and the group of genes is known as a *linkage group*.

The first linkage experiment had been done by Bateson and Punnett in 1906 and they explained it by a mechanism of coupling and repulsion. It was Morgan in 1911 who first gave the accepted modern explanation. He crossed a normal *Drosophila* with wings and a grey-coloured body with one which had vestigial wings and a black body. The F_1 was normal, i.e., grey and winged. When the male F_1 was backcrossed on to the female double recessive, i.e., with vestigial wings and a black body, the next generation gave a 1 : 1 ratio of 1 grey winged and 1 black vestigial. This is a monohybrid ratio but we are in fact dealing with a dihybrid. These results suggested to Morgan that the characters winged and grey, and also vestigial and black, were not inherited independently.

Morgan explained this result by saying that the non-independent characters were controlled by genes which were borne on the same chromosome, that is, that winged and grey were on one chromosome and vestigial winged and black were on another, and thus each pair behaved as single units in inheritance giving a monohybrid result. This experiment was thus a demonstration of linkage, and in this case the linkage was *absolute*, or complete, so that the ratios obtained were also the ratios of the chromosomes in segregation.

Linkage is an *a priori* expectation because it is obvious that, if genes control the multitudes of characters of an organism and the number of chromosomes present in any one is relatively small, then each chromosome must contain many genes which are thus linked to those chromosomes. There is in fact a very large amount of evidence for linkage and there is no need to review it. But we would like to point out a modern development which is highly important and which connects to other genetic phenomena to be mentioned later. Complex substances like vitamins, amino acids and purines are synthesized in the cell in definite chemical stages. They are built up step by step from simple initial compounds, and Demerec¹ and others working with *Salmonella* have shown that each step is controlled by a different gene, and the genes concerned are all linked, thus ensuring that synthesis normally proceeds to its complete finale. Interference with the chain of steps by mutation of any one gene results in a blockage of the reaction and an accumulation of the chemical which has been reached in the chain. There are many examples of this type of reaction which have been found in bacteria and microscopic fungi.

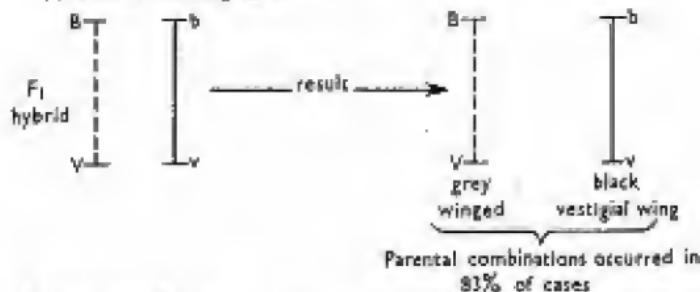
Now when the female F_1 hybrid from the cross of grey winged and black vestigial *Drosophila* was backcrossed with the double recessive male fly it was found that eighty-three per cent of the progeny were black vestigial and grey winged, whilst in the remaining seventeen per cent of the progeny these characters had been separated and new combinations of black winged and grey vestigial occurred. In the cross of the male F_1 hybrid the linkage was absolute, i.e., 100 per cent, but here in the case of the F_1 female it was only eighty-three per cent, i.e., it was not absolute. To explain this phenomenon Morgan assumed that during the formation of the gametes in the F_1 female hybrid, the chromosomes bearing these genes had twisted, a break had occurred at the twist, and the resultant portions of the chromosomes had joined up so as to form seventeen per cent of new combinations. This phenomenon is called *crossing-over*. Crossing-over is illustrated diagrammatically in Figure 15 where it is seen that in the female F_1 hybrid cross described above, four types of gametes, two normal, BV and bv , and two cross-over gametes, Bv and bV , are produced, instead of only the two normal ones if linkage had been absolute.

¹ 1935, 1936.

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Crossing-over is thus an inference from genetical data in which recombinations are produced, and its occurrence has been inferred in numerous cases. But the actual amount of crossing-over varies in different crosses. For example the F_1 hybrid between white-eyed yellow-bodied *Drosophila* with one with red eyes and grey body has red eyes and a grey body, i.e., it is the normal, or wild type, fly. When such a female F_1 is back crossed to the double recessive with white eyes and a yellow body, the progeny show

A. Without crossing-over



B. With crossing-over

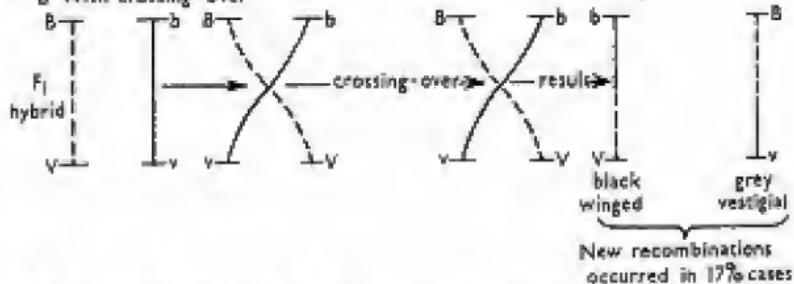


Fig. 15. Linkage and crossing-over in *Drosophila* (involving a cross of a normal fly with a grey coloured body and wings with a black-bodied and vestigial winged fly). Crossing-over results in 17% new combinations, i.e., linkage is only 83% absolute. B = gene for normal grey body colour, b = gene for black body colour, V = gene for normal winged form and v = gene for the vestigial winged form. For simplicity the chromatids have been omitted. See text for explanation.

ninety-nine per cent white-eyed yellow body and red-eyed grey bodied flies, that is, there is ninety-nine per cent linkage and only one per cent of crossing-over producing flies with white eyes and grey bodies and red eyes with yellow bodies.

Cytologically there is some observational evidence that crossing-over occurs. It is a very difficult matter to observe, but there is a large amount of inferential evidence that genetical

crossing-over does in fact occur on a cytological basis also. In several stages of meiosis the paired chromosomes are seen to be coiled round each other. As we have already observed Darlington called these points of crossing-over *chiasmata* and he held that each chiasma represented a point of genetical crossing-over. Further in the maturation divisions each chromosome is split into its daughter halves or chromatids. It is the usual opinion among cytologists and geneticists that in fact chiasmata are always physically associated with points of crossing-over, but this is not an invariable rule; for example, Cooper¹ found chiasmata in male *Drosophila* where little, if any, crossing-over is known to occur.

It has been amply demonstrated that crossing-over only occurs between chromatids and not between the whole homologous chromosomes, that is, it occurs at the four-strand stage in meiosis. This was shown by Bridges,² Bridges and Anderson³ in *Drosophila*, for maize by Rhoades,⁴ for *Neurospora* by Lindgren,⁵ to mention only a few earlier examples. Recently the single-strand cross-over at any chiasma, or point of crossing-over, was beautifully shown by Weinstein⁶ who obtained double cross-overs between two, three and four sister strands in the theoretical ratio of 1 : 2 : 1. Weinstein also remarked on the evolution of ideas on crossing-over to the effect that they were first arithmetical (ratios of genes), then geometric (location of genes), mechanical (dealing with forces), physical (effects of heat and radiation) and now they are becoming chemical, tied up with the chemical constitution of the chromosome. A simple example of single-strand crossing-over is shown diagrammatically in Figure 16.

Crossing-over has long been a puzzling phenomenon to geneticists, and indeed many complex processes must be involved in it. Modern researches are uncovering new and unexpected aspects of it. There is no need to give any of the usual examples showing its occurrence but the reader may be referred to Mather⁷ for an excellent account and more detail; we wish to consider some special aspects below. The important thing to remember about crossing-over is that it enables us to localize the gene, hence the definition of a gene as a unit of crossing-over. Various explanations of its mechanism have been advanced which we do not need to mention except that of Darlington⁸ who explained it by

¹ 1949. ² 1916. ³ 1925. ⁴ 1933. ⁵ 1933. ⁶ 1933. ⁷ 1938. ⁸ 1937.

means of the relationship between the coiling of the chromatids and that of the chromosomes in meiosis which are acted on by some little understood strains and stresses. In the last few years linkage has been shown in bacteria and phages¹ and there are also the transformations in pneumococci,² and the transductions of *Salmonella*,³ to be considered later.

Now that the chemical structure of the chromosome is becoming known, these discoveries of linkage, etc., in such lowly organisms as pneumococci and *Salmonella* render it likely that new mechanisms for crossing-over will be explored. These latest

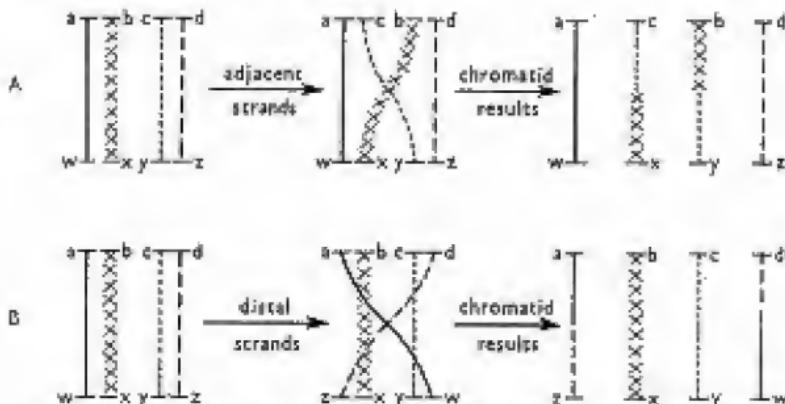


Fig. 16. Diagrams illustrating single-strand crossing-over. Each chromatid is represented differently: genes are represented by a, b, c, d and w, x, y and z. In A adjacent or inner chromatids cross-over; in B distal or outer chromatids cross-over.

views have been reviewed by R. P. Levine⁴ who discussed two new approaches to crossing-over as follows:

One approach considers crossing-over to occur along a chromosome which is nearly separated into crossover and non-crossover regions. The other, stemming from recombination studies in phage, *Aspergillus*, and *Drosophila*, leads to the idea that crossing-over occurs at a sub-molecular level. If this is true, there are two conditions under which it might occur. The first is during the time of DNA replication and the second is after this time.

The idea of sub-molecular crossing-over is new and unexpected. It should be noted that in chromosome recombinations

¹ See Lederberg, 1947; Hershey and Rotman, 1948.

² See Hotchkiss and Macmur, 1954. ³ See Demerec & Demerec, 1951.

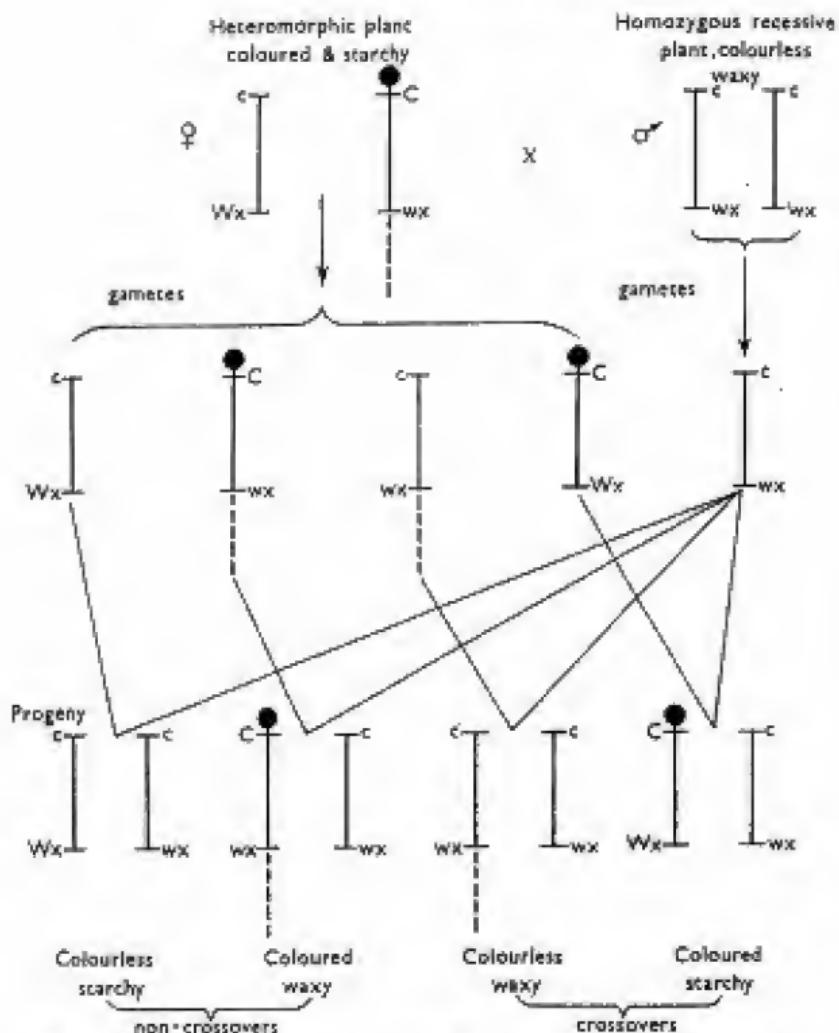


Fig. 17. Cytological demonstration of crossing-over in maize. Normal chromosome is represented as a black line, the heteromorphic chromosome has a black knob at one end and a translocated portion (broken line) of another chromosome at the other end. When the plant with a pair of heteromorphic chromosomes is crossed with a plant without a pair of heteromorphic chromosomes the result shows that crossing-over has actually occurred in that the progeny contain a form in which the knob has been transferred to one chromosome and the translocated part to another and the genes are inherited accordingly. C = gene for coloured endosperm, c = gene for colourless endosperm, Wx = gene for starchy endosperm and wx = gene for waxy endosperm. For simplicity the chromatids are not represented. (After Creighton and McClintock, 1931.)

involving crossing-over the *two* new crossover types of chromosomes are recovered together, but in phage recombinations this does not necessarily apply—only one crossover type may in fact be obtained in phages. Perhaps this may indicate some fundamental difference between crossing-over in higher and in lower organisms.

Creighton and McClintock and Stern in 1931 gave the first combined cytological and genetical evidence to show that genetical crossing-over was a result of a physical exchange of parts of homologous chromosomes. We may consider that of Creighton and McClintock. A plant of maize was produced with fruits showing coloured and starchy endosperm. The approximate positions of the genes for these characters on the chromosomes were known previously. The plant in question possessed a pair of heteromorphic (unequal) chromosomes. One member of this heteromorphic pair was normal and carried the gene *c* for colourless endosperm and the gene *Wx* for starchy endosperm. The other member possessed a large knob at one end, and, near it, the gene *C* for coloured endosperm, and also a translocated portion of a non-homologous chromosome, with the gene *wx* for waxy endosperm near it, at the other end. This plant was then crossed with a recessive homozygote with colourless and waxy endosperm, which possessed a pair of normal chromosomes carrying *c* and *wx*, and corresponding to the heteromorphic pair of chromosomes in the first plant. There were four types of progeny from this cross. Two of them resulted from ordinary segregation and recombination of the chromosomes and possessed colourless starchy and coloured waxy endosperm respectively as expected. The other two types, however, were unexpected forms with the parental characters of colourless waxy and coloured starchy respectively which, theoretically, could only arise by means of crossing-over among some of the heteromorphic pairs of chromosomes in the original coloured starchy parent. Cytologically this was demonstrated, for a clear exchange of chromosome segments had actually occurred in that the knobbed end of the chromosome carrying the gene *C* had been transferred to a normal chromosome carrying the gene *Wx*, while the other end of the knobbed chromosome bearing the gene *wx* and the non-homologous segment had been transferred to a normal chromosome carrying the gene *c*. This process is represented diagrammatically in Figure 17.

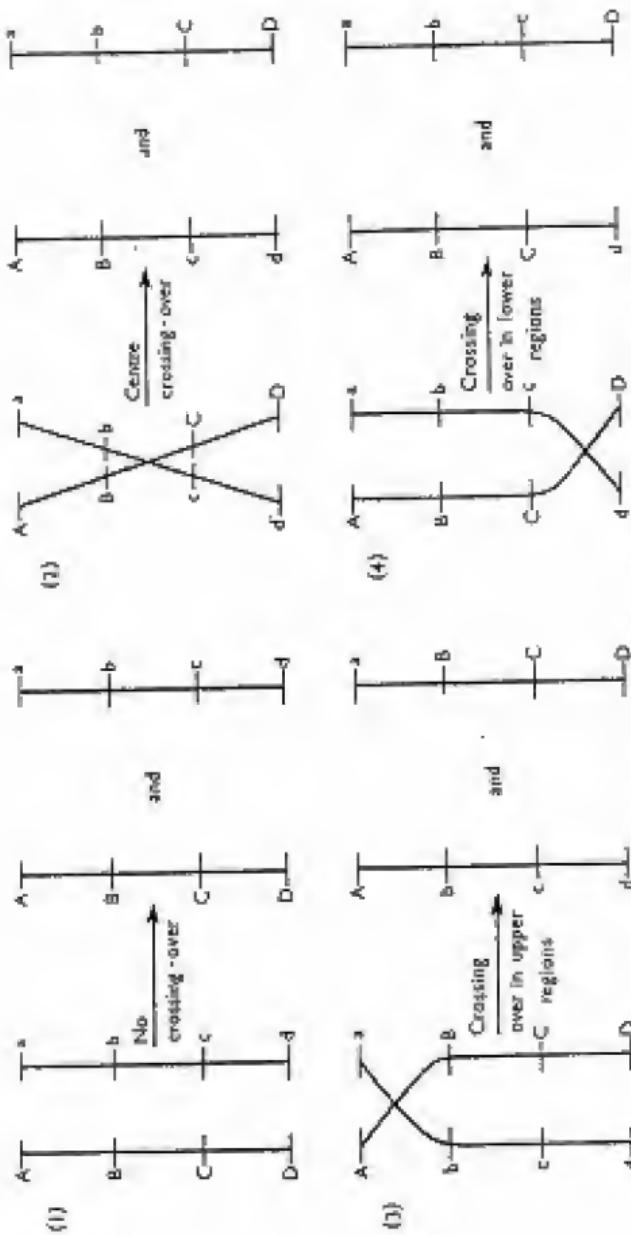


Fig. 18. Diagrams of crossing-over showing effects of distance between genes on the resultant chromatids. For simplicity the chromatids are omitted. Genes are represented by Aa, Bb, Cc and Dd. 1, with no crossing-over; 2, with crossing-over in the centre of the chromatids; 3, with crossing-over near the upper parts of the chromatids; and 4, with crossing-over near the lower parts of the chromatids.

A simple but important observation may be made from the fact that the genes are arranged linearly along the chromosomes. In crossing-over any pair of genes is liable to be separated. Thus the farther apart they are the easier it would seem to be for them to become separated. For instance consider four pairs of genes, *Aa*, *Bb*, *Cc* and *Dd* and their possible behaviour in crossing-over as shown in the diagram (Figure 18). We see that *A* and *D* are separated each time, *A* and *C* twice, *B* and *D* twice, but *A* and *B*, *B* and *C*, *C* and *D* are separated once only. Due to this difference in the amount of separation of the genes a crossover value may be given to each pair of genes, and by calculation of the crossover values for as many pairs of genes as possible the relative distance apart of the genes may be obtained. In this way genetical chromosome maps have been obtained. The most complete maps have been obtained in *Drosophila*, *Neurospora*, maize, rice, yeast and also in the mould *Aspergillus*. The importance of these maps cannot be over-emphasized because they represent a plotted scheme of inheritance in the organism concerned, and they show extremely well the possibilities and consequences of genetic recombinations which are so important in evolution. What the chromosome map shows is the locus of the genes on the chromosomes and their relative distances apart. It does not, of course, give the absolute distances between the genes. The chromosome map also shows that the gene, as the particle of inheritance, is visualized also as the unit of crossing-over which implies that no crossing-over can occur within it. Readers who wish to study a method of mapping a chromosome may consult Fothergill.¹

d. Gene action and interaction

In the early days of Mendelism a gene was a straightforward thing. The gene for red eye produced a red eye. It was considered that there was a direct cause-effect relationship between gene and character. The organism was thought of as the sum total of its genes, but this idea was never very convincing. The gene has been said to be an abstraction, a discrete particle, a unit of crossing-over, an extrapolation, a state of organization, a molecular pattern, and so on. We must not, therefore, think that a geneticist does not know what he means by a gene. Essentially the word involves a concept which has arisen from genetical

¹ 1952, Appendix 5.

experiments, and which facilitates explanation and interpretation. The concept is not rigid, and it is capable of great extension, hence the different ideas about it which indeed all arise according to the circumstances of the experiments being performed. Whether or not the gene ultimately turns out to be a thing in the true sense of that word, that is, a self-existing entity in its own right, or not, remains for the future to discover.¹ For ordinary descriptive and explanatory purposes the gene may be regarded as something situated at a point on a chromosome, and if a point is regarded as something having no dimensions, then so much the better for our conception. What matters is the locus of the point on the chromosome. The advantage of a conception like this one is that it is fluid, and the fluidity of the gene is the most notable feature of it, as we will see below. Geneticists are not to be tied down by a word.

To return to our gene for red eye. Nowadays a conception such as this is considered to be too simple and naïve. There is in reality no such thing as a gene for this or for that. Characters of organisms undoubtedly exist, and the genes merely give a measure of the character differences as J. S. Huxley² pointed out. It is thus possible to visualize conditions producing a whole series of effects such as the thirty-odd eye colours of *Drosophila* which all operate in sequence from the same point, or locus, of the chromosome bearing them. It is thus that the idea of multiple alleles arises. The normal (in the sense that it occurs most frequently), or wild, type of eye colour in *Drosophila melanogaster* is red, and all the other eye colours and mutations affecting eye colour are said to be alleles, or allelomorphic genes. The series of eye colours which range from red to white form a multiple allelic series, and, in inheritance, any two behave towards each other as simple Mendelian genes, one being dominant to the other. In Mendel's plant hybrid Tt , T represents a gene for tallness which is dominant to a recessive allele t .

We may say there is no such thing as a gene for this or for that because genes are not hermits. They do not exist alone and they

¹ The idea of 'particulate inheritance' is at present in course of considerable revision. The unit in inheritance is becoming recognised as functional rather than particulate and this functional unit is called the *siltron*. But these newer, as yet undeveloped, concepts do not really affect the validity of the standard arguments and ideas given in this account of genetics. For an account of these developing new changes in genetical interpretation the reader is referred to G. Pontecorvo (1959).

² 1942.

do not function alone. The gene is always associated with other genes forming what may be called a gene complex or an individual gene pool. It is this gene complex which provides the conditions determining the phenotype of the organism concerned. A gene in one genetic situation will behave in one way, and in another way in another genetic situation. Genes are said to be *pleiotropic*, that is, a gene may possess one primary effect and several secondary effects. A gene may also suspend its activities as it were and assume them at a later period. All these statements may be summed up by saying that genes act and interact, and the phenotype of the organism is the resultant of this action and interaction. Mather¹ stated that genes take part in three basic types of interaction as follows: (a) there is interaction between alleles which is called dominance, (b) there is interaction between non-alleles which is called epistasis, and (c) there is interaction between the effects of genes and the environment. Genic interaction revolving around these three types exists in every degree of form and complexity. Some geneticists consider that gene interaction is the result of an interaction of enzyme systems which are controlled by genes, rather than actual interaction of genes themselves.² But this refinement does not invalidate the general idea of gene interaction.

To give a complete range of examples illustrating the above statements would merely add further detail to this book which is not necessary. The ordinary examples of action and interaction of genes are found in deviations from the dihybrid $9 : 3 : 3 : 1$ ratio such as the following: the $13 : 1$, the $9 : 7$, the $13 : 3$, the $9 : 3 : 4$, the $12 : 3 : 1$, and the $9 : 6 : 1$ ratios, which depend on various arrangements of complementary, supplementary, epistatic, etc., genes. The reader may get full information from textbooks of genetics such as Waddington,³ Babcock and Clausen⁴ or Swanson⁵.

There are, however, several important effects which we should consider in more detail. Pleiotropy is now a well-established phenomenon. For example, Mendel's purple-flowered plants have reddish spots in the leaf axils, and also seeds with grey or brown coats, which are all the effects of a single gene. Dobzhansky⁶ found that the gene causing white eye in *Drosophila* also affected the length of life, spermathecal shape and colour, and the testicular membrane. While the gene *stubbloid* also affects

¹ 1955. ² See B. S. Strauss, 1955. ³ 1939. ⁴ 1927. ⁵ 1959. ⁶ 1927.

viability, antennae, legs, bristles and wings. Gruneberg¹ gave a particularly good and classic illustration of secondary effects resulting from a gene causing abnormalities of cartilage in the rat. A modified scheme of these effects is shown in Figure 19. The effects outlined in the scheme, however, are all consequences of the initial abnormality. Given the abnormality the rest follow on; whether the gene really affects the secondary abnormalities or not is not known. This is one type of pleiotropy, and another type is

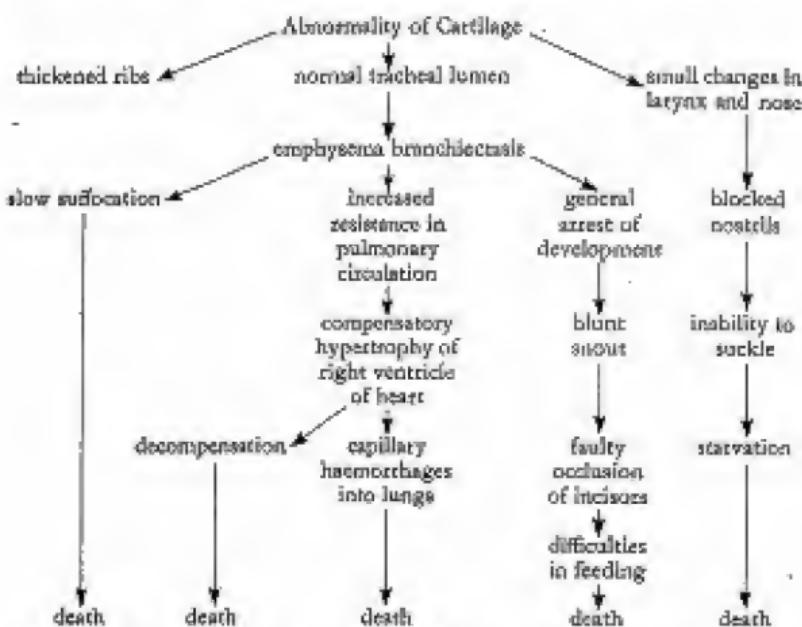


Fig. 19. Gruneberg's (1938) 'pleiotropic' effects of the gene affecting cartilage abnormality in the rat (see text).

seen where there is no necessary sequence of effects and this kind is seen when unrelated organisms are affected. Hadorn² gave detailed accounts of the effects of pleiotropy particularly regarding lethal genes. He described the 'pleiotropic pattern of manifestation' of the gene or factor which produces biochemical, physiological and morphological 'phenes', that is, sets of characters, as, for example, two lethal factors in *Drosophila* which interfere with normal protein metabolism. In lethal genes in

¹ 1938.

² 1948, 1950, 1951, 1954, 1955, 1956.

particular pleiotropy gives a distinctive pattern of damage and the effect varies according to the genetic background in which the gene is situated.

Dobzhansky¹ defined pleiotropy as follows: 'When genotypes which differ in a single gene yield phenotypes which are unlike each other in two or more not obviously related traits, this gene is said to have pleiotropic or manifold effects.' It seems that many of the series of multiple alleles may eventually be shown to be due to pleiotropic effects rather than to different or new genes.

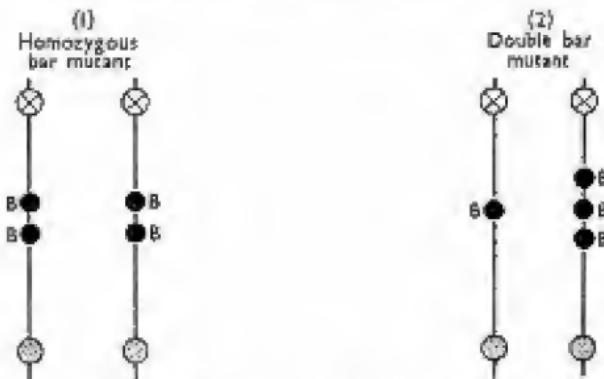


Fig. 20. Position effect in *Drosophila*, formation of 'Double-Bar' mutant from 'Bar' mutant. B = gene affecting eye-size. The presence of one B gene reduces the size of the eye; 'Bar'-eye has two B genes and the eye is smaller still. 1. = homozygous 'Bar' with two B genes on each homologous chromosome. 2. = 'Double Bar' with still smaller eyes; it is produced in the homozygous form by transfer of one B gene on one of the homologous chromosomes to the other homologue so that this one then possesses three B genes. The position of the B genes affects their expression. (After Bridges, 1936.)

Chromosomal changes and re-arrangements of various kinds will be described in the next section. If the genes are arranged linearly along the chromosomes like beads on a necklace, then such changes obviously alter the positions of the genes in relation to their neighbours. In genetics such alterations produce what are called *position effects*. The effects of the larger changes have been known for a long time, but within the last two decades a considerable amount of information on smaller position effects has

¹ 1936.

accumulated, particularly regard to *Drosophila*. And as a result it is now established that the effect of a gene varies with its position in the chromosome, that is, that adjacent genes affect the expression of a gene. Sturtevant¹ and Bridges² discovered the position effect in *Drosophila*. A gene B in this insect affects the size of the eye. When this gene is duplicated 'Bar' eye is produced and the eye is smaller. But there is a mutant called Double Bar in which the eye is smaller still. This was explained on the assumption of unequal crossing-over of these duplicated genes, so that one B gene was transferred to the homologous chromosome which thus had three B genes leaving only one in the other. The effect of this unequal crossing-over is shown in the diagram in Figure 20. The wild type had only one B gene, homozygous Bar had two on each of the homologous chromosomes, i.e., four in each cell, while Double Bar had three of the genes on one chromosome and one on the other, also a total of four in each cell, and yet the effect was different. It is clear that the proximity of the B genes to one another on the same chromosome intensified the Bar effect, that is, the effect of a gene varied according to its genic neighbours. Rapoport (1936) reported a Bar mutant apparently with four B genes on one chromosome and one on the homologue, which he called Quadruple Bar.

Many position effects have been noted in *Drosophila* by several workers; a good account of the earlier cases is given by Dobzhansky (1936). In some cases the actual genic change can be cytologically identified on the salivary gland chromosomes. Position effects, however, have been noted in only a few other organisms. For instance, Catcheside³ showed its occurrence in *Osmunda* *blandina*, McClintock⁴ showed it in maize, and it has been found in the tobacco plant. An essential point about the position effect is that the pattern of the chromosome is altered and consequently the gene reacts differently in relation to the chromosome as a chemical unit, and some modern research is concerned with this relationship. E. B. Lewis⁵ in a comprehensive review, showed that there are probably two distinct types of position effect in *Drosophila* which may not be closely related. In the first type a change in gene effect which follows the change in position fluctuates to a great extent resulting in a kind of mosaicism. In these cases both the euchromatic and heterochromatic regions of

¹ 1925.² 1936.³ 1939, and 1947a and b.⁴ 1931.⁵ 1950.

the chromosome were involved. This gave rise to a kind of 'phenotypic variegation'. This type was called the '*V*-type' by Lewis and it formed the majority of the *Drosophila* position effects. In the other kind, called the '*S*-type', the change in gene action was stable and more like a definite mutation, and it was much less frequent in occurrence. The *V*-type may be detected under certain conditions whenever a gene which is usually present in the euchromatic part of the chromosome comes to lie next to a heterochromatic part. The *V*-type gene arises in euchromatin but is influenced by heterochromatin. On the other hand, there is reason to believe that the *S*-type of effect is due to duplication of genes and to an altered positional relationship between the genes. The nature of the variegated type of position effect seems then to be intimately bound up with the heterochromatin of the chromosome, and has pointed another way which may help to solve the nature of the gene. It is known that most of the heterochromatin in *Drosophila* can be separated from the chromosomes, and L. Mather,¹ L. V. Morgan² and Goldschmidt *et al.*,³ showed, by varying the amount of this substance present in the chromosomes, that many loci could be affected. A further discussion was also given by Schultz⁴ and again by Lewis.⁵

Since about 1937 Goldschmidt⁶ has attacked the classic conception of the discrete or particulate gene. He does not consider that the chromosomes contain individual genes. According to Goldschmidt the chromosome is a definite very long chain molecule with a definite chromosomal pattern. Any alteration in this pattern produces a change in function which is known as a genetic effect. Previously such an effect has been interpreted as gene behaviour. This 'attack' on the gene at first found its greatest support from the phenomenon of the position effect. Goldschmidt,⁷ in fact, considered that it is only an alteration of the chromosome pattern which leads to evolution above the level of species; below that the small changes lead only to microevolution.⁸

The question of pseudoallelism is closely linked with the position effect because many pseudoalleles show it.⁹ Sturtevant¹⁰

¹ 1947. ² 1947. ³ 1951. ⁴ 1956. ⁵ 1955. ⁶ 1935.
⁷ 1937, 1938, 1940a and b, 1946, and 1951. ⁸ 1940a.

⁸ Research on the genetics of asexual organisms and other micro-organisms and the increase in knowledge of the physico-chemical constitution of the chromosome is beginning to substantiate Goldschmidt's opinion about the mechanism of heredity. See also footnote 1 on page 170.

⁹ See E. B. Lewis, 1951. ¹⁰ 1954, and see Lewis, 1945.

described pseudoallelism somewhat as follows: If we have a mutation $a-1$, and another independent one $a-2$, which are both recessive, then $a-1/+$ and $a-2/+$ will be wild type. But if $a-1/a-2$ possess the a phenotype, then $a-1$ and $a-2$ are said to be alleles (allelomorphic to the wild type gene).¹ This is the standard test for allelism. It means that $a-1$ and $a-2$ occur at the same locus in the chromosome and crossing-over could not theoretically occur between them. But it happens in some cases that from $a-1$ and $a-2$ two new recombination types, i.e., $a-1/a-2$ and $+/+$, can be recovered. On the usual interpretation this would mean that crossing-over had occurred between them and their sequence on the chromosome may also be shown, that is, for example, that the $a-1$ gene lies to the left of $a-2$. The double heterozygote $a-1$, $a-2/++$, is the wild or *air* type, while $a-1+/+$, $a-2$, or the *trans* type, is the recessive heterozygote. What this means is that the alleles $a-1$ and $a-2$ can both exist in the gene at the same time, that is, they are pseudoalleles not true alleles (or complete genes). The conception of pseudoallelism implies that the gene is divisible. There have been many cases of this kind since Byster² brought forward his genometric theory which postulated that every gene is composed of several sub-genes each of which produces a slightly different quantitative effect on the phenotype of an organism, and also since the Russian School³ described a similar phenomenon which they called step allelomorphism to explain the peculiar behaviour of the gene *scute*, π , which has twenty-five or so alleles affecting the frequency of bristles in *Drosophila*. The bristles were affected in groups which could only be explained on a basis of a step-wise system of alleles working in regular, but not sequential, fashion. Rafiel and Muller⁴ in fact visualized a gene complex made up of sub-genes. This is one view of pseudoallelism, namely, that the gene has several sites which may mutate independently and crossover among themselves.⁵

Another view has been advanced by several people, including Lewis,⁶ Pontecorvo⁷ and Haldane,⁸ that pseudo- or inter-alleles are different mutations of distinct chromosome regions function-

¹ The $+$ sign is used in American genetical notation to denote the wild type of gene. Thus in *Drosophila* if π represents the gene for the *scute* mutation, then a fly which shows the *scute* character will be symbolised by π , while the normal fly in reference to this mutation will be symbolised by $+\pi$.

² 1924 and 1928.

³ See Serebrovsky, 1927 and 1929; Levit, 1930; Dubinin, 1929; and Agol, 1931.

⁴ 1940.

⁵ See Pontecorvo, 1932.

⁶ 1931.

⁷ 1930.

⁸ 1934.

ally separable in the control of different steps in complex chemical reactions. The process is likened to an 'assembly line' on the chromosome, but which does not occur on the homologous chromosome. Pritchard,¹ working with *Aspergillus nidulans*, found evidence for the first view mentioned above. He concluded that what are normally called genetic or cytological crossovers may actually be the result of clusters of exchanges between a chromosome site or locus which are so close together as to be recognized as such only under special conditions. The step by step synthesis of complex chemicals in the cell provides these conditions, and it seems to be along this avenue of approach that most progress is being made. O. Winge² found a very close linkage in yeasts for the raffinose and maltose fermenting genes. He assumed that there is interallelic crossing-over between them of two kinds: (a) axial crossing-over, in which only the chromosome axis takes part and (b) non-axial crossing-over, in which a side-chain belonging to the gene molecule is exchanged for another.

Pseudoalleles are important because, like other position effects, they may point to an interpretation of the gene as something other than a discrete particle, and, if they prove to be very widespread, they may give rise to the view that all alleles are in fact pseudoalleles. A further discussion of allelism is given by Pontecorvo.³

Modern work of this kind on the gene and on crossing-over has thus given rise to many fruitful results which are of necessity a re-valuation of the classic conception of the gene in genetics and hence of its importance in evolution. There are various views and D. M. Bonner,⁴ in a lighter vein, remarked: 'I might simply say that in the case of *Neurospora* I feel that our knowledge of what constitutes a genetic unit is as yet fragmentary. We have an increasing number of facts with which to work and from these facts each one of us enjoys a certain number of fantasies.' But these fantasies are also signposts on the path of our understanding of the gene and so M. Demerec⁵ was able to sum up our knowledge of the structure of the gene as follows: '(1) Within a gene, smaller units or sites can be identified. (2) These sites have a definite minimum size. (3) Mutants representing changes at different sites of a new gene locus, although they are affected primarily in one function, may differ from one another in various

¹ 1955.

² 1933.

³ 1956.

⁴ 1936.

⁵ 1956.

new viability system (Muller)¹ in close co-operation with the physical and biological environment.²

Some cases of chromosomal alterations are given below; many of them can be induced by means of X-rays or by other means. The most evident changes involve whole sets of chromosomes and this phenomenon is called *polyploidy*. Polyploidy is of common occurrence among plants and it means that in a series of related species or forms the chromosome number is built up on a basic number of haploid chromosomes. Thus in *Solanum*³ the basic number of chromosomes is 12 and the various species in the genus have numbers of 24, 36, 48, 60, 72, 108, 120 and 144. The members of such a polyploid series are referred to as *diploids*, *triploids*, *tetraploids*, *pentaploids*, etc. In *Potentilla*⁴ the haploid chromosome number is 7 and the species range from diploid up to 16-ploid. There are very many other examples in the plant world.

Changes involving individual chromosomes are well known but fall under a few types. We have already mentioned trisomics in *Datura* where the addition of single extra chromosomes produced definite alterations in capsule form (see page 80). In *deficiencies* a small portion of a chromosome may become inert or lost. In *duplications* an extra piece carrying genes which are already on the chromosome is added to it. In *reciprocal translocation*, or *segmental interchange*, two chromosomes interchange parts. While in *inversion* a piece of the chromosome becomes completely inverted through 180 degrees, thus reversing the order of the genes in that portion. There is no need to describe how these changes are brought about, suffice it to point out that they are widespread in both plants and in animals. The reader will find detailed accounts in Dobzhansky,⁵ Huxley⁶ and Fothergill.⁶

The important thing about all of these changes is that they alter the relation of the genes to one another, and providing the resultant organisms are not sterile, they add to the possible combinations of genes in future generations.

It is fairly obvious that as nuclear division and meiosis are delicately balanced processes, any major upset in the chromosomes, such as large deletions or translocations, would probably

¹ 1949b.

² Jorgensen, 1928, Vilmodia and Simonet, 1927, 1928.

³ Shirotaival, 1930, and Munting, 1931.

⁴ 1947.

⁵ 1942.

⁶ 1952.

render the organism concerned lethal as Muller and Pontecorvo¹ suggested. As these changes are of common occurrence in wild and experimental material, it is clear that they play an important part in evolution, and this seems to be the general consensus of opinion among evolutionists. Dobzhansky² expressed this opinion very conservatively when he wrote: "The amount of chromosomal change which has taken place in evolution is much greater than has hitherto been suspected."

It seems that spontaneous chromosome change is quite common in normal plants, as, for example, in *Allium*,³ *Tradescantia*,⁴ *Trillium*⁵ and in many others. It has been suggested that natural (cosmic) radiations cause these spontaneous aberrations, but this is a difficult matter to prove. If it is probable that any abnormalities arise in this way, then their frequency of occurrence is very low.⁶ Hybridity, genetic and cytological changes such as the formation of bridges between the separating chromosomes in the late anaphase stage, are often seen to be associated with both spontaneous and induced chromosome aberrations, but the ultimate cause of them is not known.⁷

The viability of mutated genes is clearly of great importance. By viability is meant the successful negotiation by the mutant of the whole internal and external environment in relation to like and unlike mutants and species also present. Many large chromosome mutants are not viable, but both Timofeeff-Ressovsky⁸ and Gustafsson⁹ found that about two per thousand equal the viability of the parent type. Gustafsson's figure applied only to large mutations, while Timofeeff-Ressovsky's applied to both large and small ones.

Translocations induced in cultivated plants are sometimes better than the parent strain. For instance, Gustafsson¹⁰ reviewed and described several examples. The barley mutant, Erectoid 1, is stiffer in the straw than the Golden Barley parent from which it was produced by X-rays, and it has as high a yield of grain. Another barley mutant, Erectoid 7, has a yield only slightly less than the parent. In the Pea (*Pisum sativum*) O. Gelin produced a chromosome mutant with five per cent greater yield than the

¹ 1942. ² 1941, p. 148. ³ Nichols, 1941.

⁴ Giles, 1940; Bhaduri, 1942; and see Darlington and Upcott, 1941.

⁵ Bailey, 1949. ⁶ See Catchpole, 1948 and Sparrow, 1950.

⁷ See Walters, 1950; McClintock, 1949; Watanabe, 1946, etc.

⁸ 1940. ⁹ 1951. ¹⁰ 1951.

parent, while in Sweden the White Mustard mutant, called Primex, gave a greatly increased yield of 200,000 kilograms of oil which was a national gain. But spectacular results of this kind are not common, especially when the mutants are grown in the parental environment. However, Gonzalez¹ and Timofeeff-Ressovsky² showed that homozygous large mutants which did not fare so well in the parental environment often did much better in a completely new one, and this improvement was partially brought about by the presence in the mutant of modifying genes. Gustafsson considered that chromosome mutations like these may be of fundamental importance in evolution, like the very large systemic mutations.

It is becoming increasingly clear that inversions are of more importance in evolution than has hitherto been realized. They are important because actual inversions lead to irregularities in meiosis if they are crossed with the parental forms, and in many cases chromosome pairing is prevented. Thus the inverted form may be sterile with the parent and related forms. If it is heterozygous it should be self-fertile. Darlington³ seems to have been the first to point out that such inversions had possibilities for evolution because the homozygous inverted form is then reproductively isolated from the parental types and evolutionary divergence could occur if mutations took place in the inverted portion of the chromosomes.

Because of the importance of inversions a few examples are given below. The phenomenon was first described by Sturtevant in 1916⁴ who found that crossing-over was suppressed in certain loci in *Drosophila melanogaster*. He accounted for this by saying that part of the chromosome in which interference with crossing-over took place had undergone a rotation of 180°, i.e. had been completely inverted. In 1931 he found some *Drosophila* which were homozygous for this inversion and crossing-over was then restored. But the important point was that new linkage groups, that is, new gene combinations, had been produced. Inversions in plants have been found by Darlington and Gairdner⁵ in *Campanula persicifolia*, in *Tradescantia* by Darlington,⁶ in *Tulipa* by Upcott,⁷ in *Agropyron* by Ostergren,⁸ in *Paris quadrifolia* by Geitler,⁹ and even between different species in the cases of

¹ 1923. ² 1934a and b.
⁶ 1937. ⁸ 1937.

³ 1937.
⁷ 1937.

⁴ And see Fothergill, 1932.
⁵ 1940. ⁹ 1938.

Drosophila miranda and *D. pseudoboscia* by Dobzhansky and Tan¹ and *Crepis divaricata* and *C. dioecorides* by Muntzing.² Inversions have actually been demonstrated in the salivary gland cells of *Drosophila* and other flies. These cells contain specialized chromosomes which are always in an elongated state and when they divide the halves do not separate but remain attached lying side by side. Each strand in the chromosomes contains a certain number of chromomeres, that is, stainable dots, discs and plates, arranged along the strand in a definite order. The strands lying side by side are associated with each other chromomere by chromomere and the size of the chromomeres and distance apart may be tabulated and measured. In inversions in these complex chromosomes it has been noted that the order of the chromomeres in certain regions of the strands is reversed point by point. It seems to be established then that inversions and similar chromosomal changes have played a large part in the production of varieties and geographical races, and probably also of species (see also position effects, pages 173-175).

b. *Gene mutations*

A gene mutation is an alteration in a unit part or locus of a chromosome which is inherited in the Mendelian pattern. Within the last thirty years numberless gene mutations have been produced experimentally by various means involving chemicals, heat, X-rays, neutron bombardment, ultra-violet light, cosmic rays, gamma rays, etc., on a large variety of organisms including plants, insects, fungi, mice, bacteria, algae, etc.³ There is also a large variety of techniques used in obtaining mutations and in recognizing them when they are produced. Most of those which are studied in detail produce distinct phenotypic effects, but less obvious ones can be recognized and possibly these ones are actually produced in larger numbers than is usually appreciated.

Beyond the fact that some gross change took place in the gene little was actually known about its nature until recently. In 1928, the year following Muller's⁴ spectacular announcement of induced mutations in *Drosophila*, P. Griffith⁵ also published a report which

¹ 1936. ² 1934.

³ For further information see Dobzhansky, 1947, 1951; Huxley, 1941; Fothergill, 1951; and various papers in Cold Spring Harbour Symposium, 1951, by Timofteff-Ressovsky, Lewan, Demerec, Jensen.

⁴ 1927 and 1928. ⁵ 1928.

may prove to be as far-reaching for genetics and evolution as Muller's brilliant results. But little notice was taken of Griffith's work, possibly because he worked on bacteria which were not sexually reproducing. Griffith found that it was possible to obtain living encapsulated smooth (S) pneumococci from mice which had been injected with a mixture of heat-killed S forms and living non-encapsulated rough (R) pneumococci. The new S forms reproduced their own type in succeeding generations, that is, the transformation was inherited. Further, the new forms killed by heat would themselves induce their form in the R type. Thus it appeared as though a new gene had been induced in the R form. Later the experiment was repeated in culture without the agency of mice, and similar results were obtained. It was possible that the agent in the dead S coccus bringing about the change was a virus, or even that the S in the mixture contained some resistant spores which subsequently germinated.

Then in 1944 Avery *et al.* repeated Griffith's experiments using a purified extract of form S. Their purified product was able to bring about encapsulation to the R form. The extract was subjected to rigid chemical, biological and physical tests and it was found that it had the chemical nature of deoxyribonucleic acid (DNA) which is one of the main chemical constituents of chromosomes. Thus these experiments showed for the first time that a specific genetic function (encapsulation) could be established by a biological substance of specific quality. Changes like this are usually referred to as transformations rather than as mutations, and they are not mutations in the ordinary sense, nevertheless they do represent a change in the chromosomal material of the receptor strain. This work has been described by Zamenhof¹ and by Overend and Peacocke.²

Since Avery's confirmation of Griffith's work several other transformations in bacteria have been carried out, and it is now established that the agent producing the change is DNA and not any possible attachment of other protein or virus. For example, Alexander and Leidy³ induced capsular transformations in *Haemophilus influenzae* by specific deoxyribonucleates extracted from bacteria. A good deal of work has in fact been done on these remarkable inductions by several workers, but so far they have been brought about only in bacteria and about seven different

¹ 1956. ² 1957. ³ 1951.

transforming agents have been found up to the present. An account of this further work was given by Harriett Ephrussi-Taylor¹ who has formulated a working hypothesis concerning the genetic nature of transformations as follows: 'Transformations consist of the replacement of the nucleic component of an autoreproducing cell element by a nucleic acid of extraneous origin having a closely related structure and function.' While these transformations are of a particular kind, they do indicate in a general way that mutational changes are intimately connected with the genic substance of the chromosome in that DNA isolated from one strain of a micro-organism is able to transmit heritable properties to another and induce a genetic change in it.²

The action of X-rays on the chromosomes is known up to a point. Generally speaking, X-rays disrupt chromosomes and produce major killing effects, but when given in small doses they produce some gene mutations. It is now known that (a) the rate of gene mutation is linearly proportional to the amount of ionization in the tissues, (b) the mutation rate is independent of the time during which a dose of rays is given, and (c) the mutation rate is independent of the wave-length of the rays used in the process. These facts indicate that the mutation is a single event of ionization which implies a physical change in the gene.³ As regards the larger chromosome aberrations resulting from X-ray treatment of *Tradescantia* chromosomes, the work of Sax,⁴ Lea⁵ and Catcheside⁶ indicated that, given a suitable dosage, a single ionizing particle passed through the molecules of a chromosome leading to several direct ionizations as contrasted with the single ionization in the production of the gene mutation. These ionizations then broke the chromosomes, or some of them, and later the chromosome pieces joined up in new combinations, or remained un-united.

In 1947, and later in 1949, Thoday and Reed working with *Vicia faba* found that oxygen had a decided effect on producing translocations when X-rays were used, but not when *alpha* particles were used. Giles⁷ *et al.* and Katyal and Gray⁸ found that fast neutrons are intermediate between X-rays and *alpha* particles in their effects on chromosomes in *Tradescantia*. In a series of

¹ 1951. ² See also Hotchkiss, 1954.

³ See Timofeeff-Ressovsky, Zimmer & Delbrück, 1935. ⁴ 1940.

⁵ 1945. ⁶ 1948.

⁷ 1945; Giles, Beatty & Riley, 1951. ⁸ 1947.

papers¹ Giles *et al.* obtained the following results in experiments with the effects of X-rays and oxygen concentration on *Tradescantia* chromosomes in pollen grains: (a) oxygen increased the frequency of all types of X-ray aberrations immediately it was applied, (b) oxygen must normally be present during the actual X-ray treatment, (c) but there was still an appreciable amount of aberration produced in the absence of oxygen (a residue was always left in the spores), (d) between 0 and 10 per cent there was a linear increase in the frequency of aberration, between 11 and 20 per cent oxygen the frequency was more gradual, and at 21 per cent oxygen concentration a plateau was reached, (e) the increase in frequency was related to the amount of oxygen dissolved in the cells. On the basis that irradiation of water produced hydrogen peroxide (H_2O_2) Thoday considered that this substance was responsible for the chromosome aberrations. But on the basis of all the experiments mentioned, Giles² summed up the oxygen effect as follows:

The effect of oxygen during irradiation in increasing aberration frequency is found to show an inverse relationship to the specific ionization (ionization density) of the radiation utilized. Thus the oxygen effect with fast neutrons is intermediate between that with X-rays (where a pronounced effect is noted) and with *alpha* particles (where little or no effect is found). This finding is interpreted in terms of the different initial spatial distributions and consequent interactions, in the presence of dissolved oxygen, of the primary radiation products (OH radicals and H atoms) arising in the aqueous medium of cells exposed to the various types of radiations. With radiations producing a high specific ionization, radical recombinations rather than reactions of H atoms with molecular oxygen will be favoured, whereas the reverse situation will exist for radiations having a low specific ionization. Thus little effect of oxygen is anticipated with *alpha* particles, but a marked effect is expected with X-rays, and fast neutrons should be intermediate.

The primary effect of radiation therefore is to produce active radicals in the water surrounding the gene, chemical reaction then taking place whereby the gene becomes modified. The actual mutation is thus a secondary effect. Supporting evidence for Giles'

¹ Giles & Riley, 1949; 1950; Giles & Beatty, 1950; Riley, Giles & Beatty, 1952.
² 1954.

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views came from Wagner¹ working with *Neurospora*, and Haas² on bacteria, who found that mutations were produced by putting the organism into water which had been previously irradiated. While C. P. Swanson³ in collaboration with K. G. Lunning⁴ gave a comprehensive scheme regarding the breakage and the reunion of the irradiated chromosomes under the influence of the oxygen effect

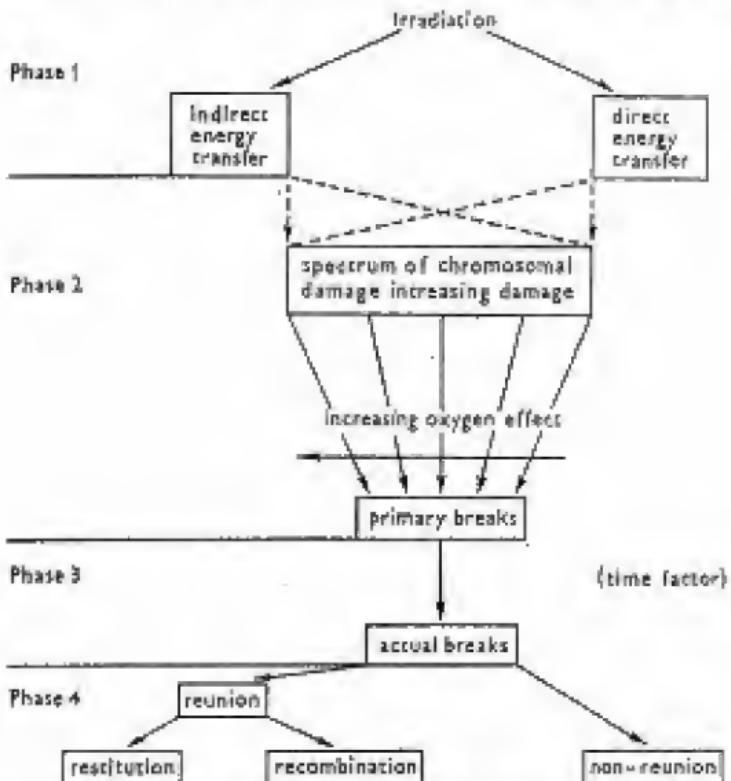


Fig. 21. Ionizing radiation effects.

as shown by Giles. This scheme, given in Figure 21, is self-explanatory and is based on a modified simplification of a scheme given in 1953 by Thoday.⁵ Swanson assumed that irradiation produces a number of primary events some of which can be repaired, while others may be further influenced by physical or chemical factors. By direct energy transfer in phase 1 in Figure 21 is meant the immediate effect of the ionizing particle on the

¹ 1950.

² 1950.

³ 1954.

⁴ 1954.

⁵ 1953b.

chromosomes, while by indirect energy transfer is meant that effect induced through ionized water. Several workers, however, have interpreted these experiments on *Vicia faba* and *Tradescantia* as meaning that the oxygen effect is on the recombination of the chromosomes when irradiated rather than on the breakage mechanism. The two interpretations are discussed in detail by Giles.¹

Induced mutations present a series of types, from those which are lethal in various early stages, through those which are weakly deleterious by reducing viability slightly, and those which are neutral, to those which are beneficial and have definite adaptive value. Some of the mutations have an extremely small effect on the organism concerned and are difficult to recognise. It is thought that an organism may carry mutated genes which in their present condition produce no effects. Nevertheless, it is generally acknowledged that the vast majority of visible gene mutations, if not actually lethal, are deleterious to the organisms possessing them. For instance, Robson and Richards² found 210 mutants out of a list of 389 given by Morgan, Bridges and Sturtevant³ were so defective as to be classed as lethal. One indication of the prevalence of these deleterious genes and mutants is that it confirms the general expectation that the larger the change in an organism the more likely it is to be harmful, and indeed Fisher⁴ has shown this to be the case. Stadler and Roman⁵ were of the opinion that irradiation in maize resulted in gene loss rather than in true gene mutation. This view was supported by Lefevre⁶ who, after extensive work, found that mutations induced by ionizing radiations, that is by X-rays, are not of the same kind as spontaneous mutations or those induced by ultra-violet light. The chief effect of the X-rays was destructive and resulted in a loss in the irradiated organism which was irreversible. If this effect occurred in many cases it could have drastic consequences for evolution if such changes were allowed to accumulate. It is clear, however, that the way in which a gene changes to a new allele is not yet known.

Superficially, then, it would seem that perhaps gene mutations could be of little use in evolution. However, soon after the experimental induction of mutations, it was found that many of the mutations produced in the laboratory had their counterparts

¹ 1935. ² 1936. ³ 1925. ⁴ 1930. ⁵ 1943 and 1948. ⁶ 1930.

in wild populations. This discovery led to the study of wild populations from this aspect by Timofeeff-Ressovsky¹ and others.² Recessive mutations extracted from wild populations showed that the differences between the various races were gene differences affecting quantitative characters similar to those produced in the laboratory, and similar to many of the quantitative characters separating varieties and species.³ Such recessive mutations occurring in wild populations are called spontaneous mutations.

The occurrence of large numbers of genes producing very small effects is now well established, and many evolutionists consider that these very small mutations are the material which brings about the evolution of species.⁴ Fisher⁴ explained the consequences of the presence of neutral genes, or of those which have only a slight selective advantage, and we quote the paragraph here. He wrote:

The very small range of selective intensity in which a factor may be regarded as effectively neutral suggests that such a condition must in general be extremely transient. The slow changes which must always be in progress, altering the genetic constitution and environmental conditions of each species, must also alter the selective advantage of each gene contrast. Slow as such changes in selective advantage must undoubtedly be, the zone separating genes possessing a definite selective advantage from those suffering a definite selective disadvantage is so narrow, of the order of the reciprocal of the breeding population, that it must be crossed somewhat rapidly. Each successful gene which spreads through the species must in some measure alter the selective advantage or disadvantage of many other genes. It will thus affect the rates at which these other genes are increasing or decreasing, and so the rate of change of its own selective advantage. The general statistical consequence is that any gene which increases in numbers, whether this increase is due to a selective advantage, an increased mutation rate, or to any other cause, such as a succession of favourable seasons, will so react upon the genetic constitution of the species, as to accelerate its increase of selective advantage if this is increasing, or to retard its decrease if it is decreasing. To put the matter in another way, each gene is constantly tending to create genetic situations favourable to its own survival, so that an increase in numbers due to any cause will in its turn react favourably upon the selective advantage which it enjoys.

¹ 1927.

² Tschetverikov, 1928; Dubinin, 1934, 1936, 1937; Gershenson, 1934; Gordon, 1935.

³ See polygenic inheritance, pp. 227-229.

⁴ 1930, p. 95.

Hence the frequency, or rate, of mutation is of great importance to their spread in a species, and hence to their effect on evolution. It seems to be considered at present that the genotype tends to change constantly and most of the changes would be due to exceedingly small mutations very difficult or impossible to detect, and yet it is these small changes which are also increasingly considered to play a very large part in evolution because their very smallness enables them to move about as it were in a population until sufficient have accumulated to exert a reasonable change in the population. Thus, in any count of numbers of mutations many, if not the majority, of these very small ones will be missed. Counts are rendered still more difficult because they may be made on species, on chromosomes, or on genes. We have already mentioned that Timofeef-Ressovsky and Gustafsson found mutations occurring at the rate of about two per thousand. This figure, compared with others in the literature, seems to be unduly high. Huxley¹ thinks that a general mutation rate of 1 in 10^5 , or 1 in 10^6 , may be expected.

So far as is known the mutation process seems to be at random, but it may only be an apparent randomness due to our lack of knowledge of the process. It is random because no major generalization has yet been formulated about it. If an organism is treated with X-rays, say, it is not known what change will occur; any tissue, or organ, or none may in fact be altered. But this statement is not true in all cases; for example, Gustafsson has shown that in barley some mutations are easily induced and controlled, and there are a few other cases. Some genes have never been known to mutate, some only once, and others mutate constantly. The following examples will show the variation in mutation frequency in different organisms. Nabours² studied the Grouse Locust for twenty years and only recorded one mutation. Stadler³ found a very great variation in the mutation rate of seven genes in maize. The mutations of the following genes per million gametes were: Wx, 0; Sh, 1.2; Y, 2.2; Su, 2.4; P, 11; I, 106; and R, 492. W. P. Spencer⁴ spent eight years studying some 7,589 pedigree cultures of *Drosophila funebris* and *D. hydei* numbering a total of 750,000 flies. He found that the rate of spontaneous mutation varied greatly and for a continuous period of thirty-eight months no mutations were observed. Timofeef-Ressovsky⁵ X-rayed an

¹ 1942. ² 1930. ³ See Waddington, 1939, p. 381. ⁴ 1935. ⁵ 1932.

American and a Russian Race of *Drosophila melanogaster* and found that the American Race produced fifty-five mutations from red to white eye colour involving 39,200 flies, but the Russian Race only produced forty similar mutations in 75,300 flies.

When Fisher produced his fundamental theorem of natural selection it was not realized that many very small mutations might be produced frequently, and his calculations were made on the basis of the known mutation rates of ordinary gene mutations. Even so he found that in general in *Drosophila* mutations are seldom produced more than once in 100,000 individuals. If there were no selective survival it would take 100,000 generations to produce an important change concerning the mutation in the genetic constitution of the species. If the gene were opposed by a very small selective disadvantage the change would soon be brought to a standstill. With a selective advantage as low as only one per cent the genetic constitution would be greatly modified in only 100 generations. But if a mutation persistently occurring once in 100,000 individuals is opposed by a selective advantage of one per cent equilibrium will be established in the population when 1 in 1,000 individuals are affected by the mutation. Fisher concluded: 'For mutations to dominate the trend of evolution it is thus necessary to postulate mutation rates immensely greater than those which are known to occur, and of an order of magnitude which, in general, would be incompatible with particulate inheritance.' He considered that mutations did not affect the course of evolution and that we are then left with only selection as an effective agency. This does not mean that mutations have to be abandoned, they do after all produce direct changes in organisms; it only means that our knowledge about them was not then sufficient to give an explanation. The paradox thus created was rendered greater when it was realized that in nature most wild type genes are dominant, while the vast majority of mutant genes are recessive—only a few dominant mutants have been produced. For example, in *Drosophila* over 200 genes are recessive and only a dozen or so are dominant.

In order to play any significant part in evolution the recessive advantageous genes, or mutations, must become dominant sooner or later and compete on an equal footing with the original genes, and further, they have to do this in the teeth of a mass of dis-

¹ 1930, p. 20.

advantageous genes. Such advantageous genes would for the most part be present in the heterozygous state, i.e., in combination with the wild type. In such a state that gene complex which manifested the advantageous genes to the best advantage would generally be naturally selected, and the greater the manifestation of advantage the greater the selection would act. It is generally supposed that a new mutant gene would in the course of time become dominant to the original wild type and would supplant it. This argument, of course, presupposes that the original gene remains stationary in terms of selective advantage, which may be unlikely. To be really able to compete with the wild type gene a mutant gene must increase its quality of advantageousness which it confers on the species until this quality is greater than that of the wild type gene. It has yet to be shown that selection can do this. In any case the many more disadvantageous genes which are produced have yet to be accounted for.

To overcome the paradox Fisher¹ evolved his theory of the evolution of dominance. The argument for this may be stated briefly as follows. Practically all mutants when they are first produced are present in the heterozygous state. Those that tend to be dominant producing definite phenotypic effects will tend to be adversely affected. If mutations are produced repeatedly then the presence of genes modifying the expression of the mutant will be advantageous to the organism. In the course of time, through the operation of these modifying genes, it can be expected that the mutant gene will become pushed into recessivity by the selection of the genes modifying its action. Thus eventually the disadvantageous mutant comes to resemble the wild type until it ceases to have any disadvantageous effects on the organism. This is the theory of dominance. Hence the theory depends on a selection of the environment of the mutant gene so as to prevent the gene from producing a bad effect on the mutant organism. Evidence for the theory is derived from the known reaction between genes and there are many known cases in which certain genes reduce the dominance of other genes.

Fisher described the case of the cotton plant as showing evidence of the presence of modifying genes. This work was

¹ 1928, 1937, 1934, 1935; Ford, 1930.

done by Harland¹ and others. Sea Island Cotton repeatedly produces a mutation called crinkled-dwarf which is recessive to the normal form in the species. The New World Cotton species, however, do not naturally possess this mutant, but Harland introduced it into them and found that in the F_1 generation it was no longer recessive. The dominance of the wild type had consequently been reduced. In the F_2 generation, however, there was an almost continuous variation in regard to dominance and recessiveness of this gene. This was interpreted to show that Sea Island Cotton contains a number of genes modifying the dominance of the gene for crinkled-dwarf. Another interesting example in cotton described by the same writers concerned the inheritance of petal spot which shows a blending type of inheritance rather than the clear-cut Mendelian kind. *Gossypium barbadense* and *G. hirsutum* both possess varieties with and without purple petal spots. In each species the presence of the spot is dominant, but when they were crossed the F_1 had only a small spot, while the F_2 showed plants with large spots, some with small spots and some with various intermediate-sized spots. By back crossing to the original parents the parental type of spot was produced again. Harland analysed these crosses and postulated a gene S^p for the presence of the spot and s^p for its absence and also a number of modifying genes in *G. barbadense* which made the spot large, and a number of different modifying genes making it small in *G. hirsutum*. In the F_1 hybrid then the interaction and segregation of these genes and their modifiers gave a large swing of variation.

Fisher's theory of dominance was a brilliant attempt to overcome a great difficulty in the application of genetic theory to evolution, but it was drastically criticised by Wright,² Haldane,³ Muller⁴ and others. Its greatest drawback, in spite of Harland's example of modifying genes in cotton, is that it implies that, for every new mutant gene produced, a corresponding quota of modifiers must also be formed. These modifiers must obviously be themselves suppressed by others and so on *ad infinitum*.

However, it seems to be firmly established now that to some extent the terms dominant and recessive as we normally use them

¹ 1932a and b, 1935, and 1936; also Hutchinson, 1934; Hutchinson and Ghose, 1937, and Sulow, 1939a and b.

² 1939.

³ 1930.

⁴ 1932.

are arbitrary terms. It is true that no one factor is completely dominant or recessive. The recessive modifies the dominant and the dominant modifies the recessive. What is important is the whole genotype, and, after all, the idea of modifying genes is merely an extension of genotypic *milieux* to explain the facts. Lerner¹ recognised the difficulty of the theory of dominance and pointed out that, if dominance modifiers (which are genes on other loci of the chromosome) are already present before the mutant is produced, and if they do not differ in their primary functions, then they can be viewed effectively as homozygous genes which may vary in their secondary effects affecting dominance. Hence, if a mutant arises, the secondary effect is ready to be brought into force immediately under the action of selection.

In conclusion we may remark that mutations present a problem to the evolutionist, and yet they are the seemingly obvious raw material on which evolution could work to produce change and variety. J. Huxley considered that the direct and complete proof that mutations are utilized in evolution has not yet been given, but the evidence that they play a large part in this process is cumulative in spite of difficulties over the 'how' of the process. Nearly twenty years ago Huxley² wrote:

The detailed analysis of the last ten or fifteen years, however, has revealed large numbers of gene differences with extremely small effects, down almost to the limit of detectability. It is not only possible but highly probable that among these are to be sought the chief building-blocks of evolutionary change, and that it is by means of small mutations notably in the form of series of multiple allelic steps, each adjusted for viability and efficiency by recombinations and further small mutations, that progressive and adaptive evolution has occurred.

Recombination alone, while it may produce a very large number of new combinations, is limited in its effects. Its potentiality is greatly increased by the introduction of new genes.

¹ 1954. ² 1942, p. 175.

Chapter VI

Modern Evolutionary Theory, Continued

I. ISOLATION

THE importance of isolation in evolution became recognized in the early Darwinian days. In 1867 Jenkins criticized the Darwinian theory by pointing out that a naturally selected favourable variation would be swamped by breeding and lost as an effective agent in evolution. This difficulty no longer applies in the light of modern genetics, but at the time it raised a real problem. It was partially overcome by Moritz Wagner¹ in 1868 who considered that, due to an innate tendency to migrate into new areas, animal populations became separated into smaller geographically isolated groups where natural selection could play its part and where the chances of swamping due to crossing would be greatly reduced. Later, in 1887, Gulick published a theory of isolation. Gulick recognized two kinds of evolution, (a) monotypic evolution, that is, evolution without change of type, and (b) polytypic, or divergent, evolution with change of type. It is the latter type which he considered accounts for the real evolution of species. Gulick recognized eighteen different kinds of isolation, most of which effectively brought about a differential reproduction within the species. Romanes² also gave a detailed treatment of isolation as an agent in evolution. Although an ardent Darwinian, he recognized that selection alone could not account for the whole process of evolution. He emphasized a form of physiological isolation which prevents interbreeding between variants and parental forms.

Since these earlier ideas isolation has become universally recognized as of major importance in evolution. The word is self-explanatory, and it is not necessary to give a detailed account here. Only a cursory outline of the chief ways in which isolation is brought about will be mentioned. Isolation in evolution means any mechanism which effectively prevents cross-breeding between the individuals of a species. In this way new varieties (mutants,

¹ 1868a and b. ² 1897, Vol. 3.

etc.) are given a chance to extend and stabilize themselves. If cross-breeding is constantly taking place a population may reach a position of equilibrium and so becomes static in an evolutionary sense. The mere multiplication of types does not necessarily lead to genetic differences of evolutionary value in a population. So that changes in members of such a population may have little chance of contributing to evolution.

Isolation brings about divergence between varieties and species, and if it is a spatial isolation such divergence works in an altered selection pressure in the isolated portions of an area. There are many examples of geographical distribution of species showing the effect of isolation. It is well known that species ranging over a very wide continental area show a large number of sub-species and varieties each related to their own geographical niche. In some cases there is a continuous gradation of forms of a species from one extreme of the area to the other with well-marked differences in the varieties inhabiting the extremes of the area. But in the general case distribution regions of varieties or races do not overlap and this fact is well seen among groups of islands where the variation is much less in the central part of the group and much greater towards the periphery.¹

There are two main types of isolating mechanisms, namely, geographical, or spatial, and biological isolation. The latter type may be conveniently sub-divided into (a) ecological isolation, (b) physiological isolation and (c) genetical isolation.²

In geographical isolation plants are more affected than animals because they are sedentary and depend for extension of their distribution on the various seed and fruit dissemination methods. On the large scale geographical isolation is obviously brought about by hills, mountain chains, rivers, lakes, oceans, etc. In some cases the isolation may be absolutely complete, but this is probably rare. Even mountains and seas are sometimes crossed by some species. These barriers are, however, generally efficient, but even so they do not account for all of the cases of divergence of species brought about by spatial distribution. Schmalhausen³ considered

¹ See also geographical distribution, p. 141, *et seq.*

² For good comprehensive modern accounts of isolation and speciation the reader may consult Dobzhansky, 1941; Mayr, 1942, 1949; Schmalhausen, 1949; Lack, 1949; Ford, 1949, 1954. For an account of the earlier theories of isolation consult Fothergill, 1952.

³ 1949.

that the more limited partial isolation which only reduces cross-breeding without preventing it is of great importance and is inherent in the mere fact that individuals (chiefly sedentary ones) occupy different actual positions. He wrote: 'At the same time, this partial limitation, which permits a rather extensive interchange of individuals of different populations, has considerable progressive value, for it helps preserve the plasticity of the organism and the capacity for a more rapid tempo of evolution.'

Thus geographical or spatial isolation, according to the degree in which it is operative, prevents, or tends to prevent, mating between certain individuals and groups of individuals. Inevitably this causes a species to be broken up into a number of distinct races and sub-species. According to Mayr¹ a species is a reproductively isolated group of populations, and hence geographical isolation will only initiate the process of true speciation, that is, splitting of one species into two or more species, because mere spatial isolation need not necessarily mean actual reproductive isolation which prevents cross-breeding no matter how far apart the organisms are. If the barrier preventing interbreeding is a small one, and is removed, interbreeding may occur unless there is also some form of reproductive isolation. Thus geographical isolation produces varieties which are really antecedent to species formation. The importance of geographical isolation in evolution is that it provides the environment in which isolating mechanisms actually preventing reproduction between related forms may be developed.

The truly isolating mechanisms are provided by the various cases of biological isolation. Indeed, geographical isolation is also directly connected to the biology of the organisms concerned. Species may be separated not only by distance, but also by some ecological or physiological reasons present in the different areas of distribution. In many ways ecological and geographical isolation overlap and are sometimes difficult to separate. Ecological isolation includes all those features of an area such as type of soil, light conditions, altitude, temperature, depth of water for aquatic species, etc., and, more particularly, features such as seasonal divergence of races, and differences in mating times and so on.

Physiological isolation, broadly speaking, includes any barriers within the organism which prevent breeding of a variety with the

¹ 1942, p. 247.

parents or its like, but which does not render the variety sterile *inter se*, due to some physiological or morphological change in the reproductive and similar systems. If the sexes become incompatible for some reason such as differences in the structure of the genitalia, which is often seen in insects, or for some other similar cause, a differential fertility is set up between the varieties of the species which does not prevent them reproducing each with their own variety, but does prevent cross-breeding between the parents and other varieties. In higher animals physiological isolation of a similar kind is seen in what is called psychic isolation due to some mental reason preventing actual mating. There may also be biochemical isolation produced by failure of sex glands to develop properly in sterile hybrids, or chemical differences preventing actual conjugation of the egg and sperm, or the pollen nucleus with the ovule nucleus, or the growth of the pollen tube, etc. Apparently in some animals at least, such as *Microphylla olivacea* and *M. carolinensis*, size difference is a mechanism affecting interbreeding between two species.¹ Genetic isolation is really a type of physiological isolation but is sufficiently different to the other types of mechanisms operating under this heading to warrant separate mention. The appropriate mechanism here includes all disturbances of meiosis leading to irregular divisions, such as lack of conjugation between the chromosomes. Genetic isolation also results from what is called genic sterility in which a gene controls the viability of the organism.² Sterility due to chromosomal aberrations are often ultimately caused by alteration of the gene sequence on the chromosomes. Genetic and cytological features such as aneuploidy and polyploidy are also sometimes responsible for much genetic isolation among populations. Many of these features have already been dealt with in Chapter 5.

Without going into any further detail we may say that isolation in all its various forms must play a vital part in species evolution. When a species becomes subdivided into partially isolated local groups a great store of variability is built up in the species compared to the amount of variability in a random breeding population where there is little isolation. This isolation changes the selection pressure on the genetic complexes of the species and overcomes the difficulty of lack of substantial evolutionary change due to the rare occurrence of favourable mutations. In the isolated population

¹ See W. F. Blair, 1933.

² See Dobzhansky, 1942.

genetic changes occur due to any favourable mutations and recombination of genes. The isolated population becomes stabilized through changes in the reproductive mechanisms and once this condition has been attained future mixing with other varieties does not swamp them, but increases the chances of further divergence due to gene flow. Wright¹ considered that under an interpretation of this kind 'a continual kaleidoscopic shifting of the statistical characteristics of the local populations is to be expected within any species that occupies, not too densely, a reasonably large range. A similar but slower shifting of characters is to be expected among the larger and more differentiated groups recognized as subspecies. The net result should be a gradual shifting in the characters of the species as a whole until the change becomes so great that a new species must be recognized. Subspecies on this view are only rarely incipient species.'

Wright's conception of speciation depends on partial isolation of small groups producing what he called genetic drift due to accidental sampling of the larger population.² On the other hand, David Lack³ took a wider view of isolation and considered that the origin of species is bound up with adaptive radiation, and he stressed the importance of ecological isolation rather than genetic isolation. In this process he gave the links in the chain as follows: '(a) geographical isolation of populations, (b) morphological differentiation, (c) partial inter-sterility and partial ecological divergence, (d) re-meeting, with persistence of each form as a new species when both genetic and ecological isolation are sufficient, (e) increased ecological restriction and differentiation and increased specialization of each form to its modified niche, and (f) further geographical spread of each form, with a repetition of the whole from (a) to (c).'⁴ In this way isolation can be seen to begin a process of adaptive radiation which continues as the radiation expands; thus evolution forges ahead.

2. SELECTION

A. General account

The modern causal evolutionary theory is largely genetical, and much of it is theoretically based on statistical considerations. While it still includes the old idea of 'natural selection', this tenet of the

¹ 1949b. ² 1951. ³ 1949, p. 308.

old Darwinism has now found its rightful place as one of the most important factors of evolution. The modern theory is not merely a resuscitated Neo-Darwinism, it is in fact very different from the original Darwinism. Its material is drawn from many sources which were unknown to Darwin. The older idea of small advantageous and almost individual variations continuously and unidirectionally selected over a long period of time, or of the incessant struggle between species, has really been largely superseded. The poetic idea, for instance, of nature 'red in tooth and claw' is anathema to the modern evolutionist. The strength and appeal of the modern evolutionary theory lies in its connection with the chromosome theory of heredity, and it tends to regard the adaptive or evolutionary unit as a population rather than as an individual. Usually the individual only plays a relatively minor role in evolution, and selection of individuals thus no longer has the force which it was once thought to have. This statement, of course, does not imply that sometimes one or two individuals may not produce a new form, for this in fact is known to occur. There is nothing in evolutionary mechanisms so far as is known to prevent a single (or a pair) of individuals from directly producing a new line in evolution (see footnote 2, page 230). Selection, of course, still operates, and is of very great importance, but it is not looked upon so much as an agent of elimination as one which brings about a differential reproduction among members of a group and so tends to produce a shift in the modal expression of that group, thus leading to change and evolution.

Some very keen modern evolutionists, however, still tend to revere selection to some extent. Indeed, G. G. Simpson¹ considered it to be a creative factor in evolution, when in reality it has nothing to do with origins except remotely because it can only operate on things already in existence. Some evolutionists are very dogmatic and rather confused in their meaning here in a subject which so clearly bristles with factual, emotional, methodological, linguistic and even scientific difficulties. For example, J. Holmes² wrote about the 'creative role' assigned to selection; while of those who say that natural selection originates nothing, C. C. Nutting³ remarked: 'I must confess to scant patience with this view.' On the other hand H. J. Muller⁴ considered that it is semantically confused to dispute whether natural selection is

1 1950.

† 1948.

* 1921.

* 1949.

creative. It obviously depends on the meaning we give to the word 'creation', which is true enough; but this word has always had a precise meaning with fundamental connotations. Muller contended that natural selection, by eliminating the unfit, sets the conditions for the fit to become actual (there is a play of words here, because both the fit and the unfit are actual before selection operates). Muller asserted that this process is more 'creative' than the sculptor who creates his statues, or the poet who writes his poems. He said the image in a sense was latent in the block of stone. But it is precisely such a misuse of words and concepts which renders evolutionary theory so unpalatable to many non-biologists. The image of the statue is latent only in the mind of a *conscious* sculptor and without him there could never be any statue; but whether the statue is ever made or not, the image could continue to exist in the sculptor's mind. Creation is ultimately the work of a rational conscious being and finally connects to the production of something out of nothing by the Creator. It would seem to be preferable to limit the meaning of the word to this unique work rather than to use it in what can only be a completely different sense, unless its use in this sense is clearly indicated. Creation by selection is a derived and not a primary effect.¹ Otherwise a semantic confusion of the selectionist's making tends to arise. Those who deify selection in this way are playing a dubious game because they may produce a wrong impression in the minds of people who read their writings and who have not sufficient background to counteract the implied suggestion of the use of the word to represent a primary creative agent. Such people then tend to equate selection in their minds with the Creator. Such false or weak analogies do not lead to clarification and progress.

As the modern theory of evolution progressed it has become noticeable that the place of selection in it has receded and at the same time has become stabilized and clarified. The original idea of selection was that of a concept covering everything which affected the organism, and hence it was a truism and was rendered meaningless to a considerable extent. But out of it arose the work which now analyses the internal and external environment of the

¹ The word 'creation' is properly used in three ways: (a) absolute creation by God alone, (b) derivative creation or creation through the action of secondary causes and (c) creation by rational man (see Mivart, 1871).

organism, and it is this analysis which shows that there is no single causal factor of evolution, but instead a multitude of forces and actions producing effects, the resultant of which we call evolution. This position which evolutionary theory now occupies has been brought about largely by genetics and its mathematical analysis, and the co-operation of all types of biologists such as ecologists, cytologists, morphologists, etc. This advance in evolutionary theory was ably summed up by one of the foremost mathematical selectionists as early as 1932, when the modern theory was just beginning to be visualized. Sewall Wright¹ wrote:

Summing up, I have attempted to form a judgment as to the conditions for evolution, based on the statistical consequences of Mendelian heredity. The most general conclusion is that evolution depends on a certain balance among its factors. There must be gene mutation, but an excessive rate gives an array of freaks, not evolution; there must be selection but too severe a process destroys the field of variability and thus the basis for further advance; prevalence of local inbreeding within a species has extremely important evolutionary consequences but too close inbreeding leads merely to extinction. A certain amount of cross-breeding is favourable but not too much. In this dependence on balance, the species is like a living organism. At all levels of organization, life depends on the maintenance of a certain balance among its factors.

And while Wright regarded selection as the guiding principle of evolution, the recognition of a necessary balance of the factors involved represented a great advance on the older position. In selection theory a distinction should always be made between the operation of selection and the mere ability of an organism to live in adverse circumstances.

The use of mathematics in physics and chemistry is well understood and its position is clear; but in biology generally the place of mathematics stands in a different relation to its use in all the sciences on inanimate objects. A criticism of R. A. Fisher's use of mathematics in biology and of his fundamental theory of natural selection which has been generally overlooked was given by W. R. Thompson² who pointed out that the use of mathematics in biology furnishes us at best with a mathematical analogy, and even when properly stated and posed the analogy strips the

¹ 1932. ² 1937, p. 124.

biological situation of one of its most specific characteristics. As far as evolution is concerned the chief characteristics are those of the self-regulatory power of the organism and the fact that it is a co-ordinated unity. As Thompson said: 'In short, mathematics is not a substitute for experiment; neither is mathematics experimental. It is not necessary to go to Nature to demonstrate the truths of mathematics. On the other hand, this essential independence of mathematics in regard to Nature prevents it, in a sense, from getting any real hold on Nature. Only observation and experiment can tell us what really happens.'

Nowadays it is generally agreed among evolutionists that while many factors operate in the evolution of species, the four most important ones are mutation, recombination, isolation and selection. It is probable that these factors may have to operate continually before any permanent change may be produced in the species. If one of the factors is absent or in abeyance, in any particular case, then evolution in that case might cease—the population of individuals concerned would become largely static. Put shortly we may say that mutation is the source, or basic origin, of new, possibly evolutionary, material; recombination incorporates the new mutation into the established system; selection gives direction to the effect of the new material if it has adaptive value; while isolation enables the new material to become established, allowing it later to evolve along its own lines. While all these factors operate in evolution, and as Sewall Wright said, a proper balance between them is necessary, it is easy to see how selection came to be regarded as the guiding force, or even as a 'creative' factor, because during the long time scale of evolution many mutations may arise and all combinations of them among themselves and among the stock already in existence may occur, but it is selection which determines the response of the combinations in any environment. Selection thus becomes the directive of evolution. It should be remembered that the organisms which are being selected are themselves a part of the selective process. The interaction of organisms with each other, and with their environment, produces selection. Thus selection '*per se*' is an end result rather than a beginning, but in the complex *milieu* of living things selection appears to be in continuous operation as a process or active agent always present. Such an agent is not one which could work by chance—selection is in fact

very probably a law-abiding process, which feature becomes more and more obvious as research on evolution proceeds.¹ We may say that, to the biologist, evolution in the past simulated a chance process because of the too dominant position given to the selective factor, and because of the extreme complexity of the evolutionary mechanisms—no biologist today would be rash enough to claim that we have solved evolutionary problems; he would more likely say we have only touched the fringe. Chance arises in evolution in the sense that any new mutation which appears is untried and its effect unknown. The laws governing the production of mutations are not by any means known, and until they are and demonstrate the process beyond doubt, then there is strong *a priori* probability that they arise in response to definite productive conditions and for definite reasons.

Dobzhansky² pointed out that selection theory is essentially one of the mechanisms of *adaptation* of organisms to their environment and only secondarily a theory of evolutionary *causation*. Because selection seems to be such a guiding force in evolution many modern evolutionists tend to equate the phenomena of adaptation and evolution. They consider that a demonstration of the way in which an organism has become adapted to its surroundings gives evidence of the way in which it has evolved, which is true enough but may not be the whole truth. The term adaptation as used above involves two distinct biological concepts which are difficult to define³—these are *adaptedness* and *adaptation*. An organism may be adapted to a set of conditions in a given environment, but may not possess the means of adaptability to another environment. Adaptedness is sometimes equated with fitness to live in an environment and with selective value which is a measure of selection because the ability of an organism to survive indicates that selection has acted positively on it. Adaptedness is a quality, while on the other hand an adaptation, strictly speaking, is the characteristic which gives adaptedness. Thus the origin of adaptations in the fuller sense is concerned with the genes in an organism in conjunction with their ability to survive in which selection is the guiding factor. When adaptedness is progressive and includes also adaptability, then adaptation becomes a major

¹ This important point about selection was strongly emphasised by de Beer (1958), Introduction. See also p. 46 and pp. 309-311.

² 1941, 2nd ed., p. 187.

³ See Dobzhansky, 1955, p. 11.

criterion of evolution. And so R. A. Fisher¹ could say 'For rational systems of evolution, that is for theories which make at least the most familiar facts intelligible to the reason, we must turn to those that make progressive adaptation the driving force of the process.' As this driving force is considered to be overwhelmingly that of selection, we can see again how important selection is in evolutionary theory.

Up to the present, however, we have only indicated that selection theory in evolution arose as a deduction made initially by Charles Darwin from the facts of overproduction, variation, etc. It is necessary now to examine some of the evidence for the actual occurrence of selection in nature. The grosser kinds of selection, such as the struggle for existence and competition between species, are practically self-evident in nature, but these, while effective in evolution up to a point, are only one manifestation of selection as a whole. Competition as such may also in some cases tend to eliminate both good and bad variations rather indiscriminately, and its long-term effects are thereby nullified. It is at this point that the original Darwinism parts company with its modern developments.

The evidence that selection operates in nature is obtained from various sources. Some of it concerns observations made on a few individuals, or on populations, in the natural state, while some of it is indirect, carried out on organisms in the laboratory. The difficulty regarding selection experiments in the laboratory is to be sure that the effects of artificial selection have been eliminated. In practice it is often difficult to be certain of this. The aim of the observations, both direct and indirect, is to determine whether one type of organism is somehow chosen so that it is given a preferential death rate as against another type which is selected against. There is not a great deal of direct evidence for natural selection because it is difficult to obtain precise results especially under natural conditions where so many, perhaps extraneous, factors are in operation. Nevertheless there is a quickly growing mass of information both of the laboratory type and of the field type. The former type is often concerned with artificial selection, that is, man-made selection, but there is obviously an analogical relation between natural and artificial selection, but the analogy must not be stressed too far. It is reasonable to assume that a

¹ 1936.

measure of one type of selection may furnish a measure of the other type, and the effects of one type may be used to assist in the formulation of the effects of the other type. Rigid proof of selection is almost impossible to obtain in any particular case, and while selection is not evolution, this fact applies even more so if selection is regarded as a causal agent in evolution, because to show that the selective process has in fact changed a race of organisms in an evolutionary sense involves so many factors which it is exceedingly difficult to consider simultaneously in any one case.

Nevertheless, some time this difficulty will have to be overcome. This important problem is well stated by Mather¹ who wrote:

We must therefore aim at arranging our observations so that certain of the factors may be eliminated from the immediate consideration, or may at least be the subjects of plausible assumption. In this way we may seek to analyse and discuss the effects of the various agencies a few at a time, though we must never forget that ultimately the full complexity of their interplay must be faced. Our device of materials and experimental procedure will be governed by these considerations.²

Hence, generally speaking, the evidence for natural selection is partial in any one case, but *in toto* it is cumulative. In actual practice the conclusions drawn from selection experiments or observations often depend on the argument that unless selection be granted then the attainment of some explanation becomes impossible or unreasonable, while, granted selection, a perfectly reasonable scientific explanation becomes possible and leads to further clarification of the issues involved. It is just as well to bear in mind here that few responsible scientists claim that such a scientific explanation is necessarily the ultimate explanation, although, of course, it may be.

Before giving an account of actual evidence for selection we may state the criteria which are, of course, the yardstick by which all experiments on selection should be judged. These have been stated by Mather and by Pearl. We have already quoted Mather's summing-up regarding his criteria. Mather,³ in line with modern practice, was concerned with the effects of selection on populations, not on individuals, and he maintained that the response of a population to selection depends on three sets of factors. These are: (a) the types and strengths of the selective forces in operation;

¹ 1955, p. 158.

² See footnote 1, p. 270.

³ 1955.

(b) the action and interaction of the genes producing the effects, because, while the outward effect is seen in the phenotype of the population, the transmission of the effect lies in the genotype; and (c) the amount, distribution and system of genetic variability in the population. Pearl¹ formulated his criteria as the logical requirements for a proof that selection has actually changed a race or variety. There are five of them, as follows: (a) proof of somatic differences between survivors and eliminated; (b) proof of genetic differences between survivors and eliminated; (c) proof of effective time of elimination; (d) proof of somatic alteration of a race; and (e) proof of genetic alteration of a race.

The ultimate demonstration of the effectiveness of selection in evolution still seems to be wanting. As far as we know no single investigation of a particular case of selection has satisfied or included all of Mather's and of Pearl's requirements. It is open to argument, of course, whether all of these criteria need be stringently and simultaneously satisfied. Modern selectionists often define evolution in a limited sense to suit their purpose. If they show, either practically or theoretically, that a population has changed, that is evolution, and it is true. But that is not evolution in the more complete sense of Darwin of an ultimate descent of all organisms from one or a few primordial ancestors. Thus, much of modern selection theory assumes the occurrence of all but a limited type of evolution, it assumes selection to a certain extent and it assumes the effectiveness of small changes in species on a long-term basis. Its success lies in the fact that it is able to give a satisfactory explanation of change in nature, but the methodological process it involves is finally deductive not inductive and is completely dependent on its premisses. Other deductions based on the same experiments and observations, but on different premisses, are possible and in fact have been advanced.²

B. Evidence for the occurrence of selection

(a) Earlier observations and experiments

The main lines of evidence for the occurrence of selection will be briefly reviewed here.³ Previous to the formulation of the theory of the gene by Morgan several of the earlier Darwinians made

¹ 1930

² See Goldschmidt, 1940a.

³ Detailed accounts will be found in Robson & Richards, 1936; Dobzhansky, 1941; and Fothergill, 1952.

observations in nature and performed experiments purporting to show the action of selection. The chief of these, stated in chronological order, are as follows.

In 1896 Kane claimed to show that there was selection for a black variety of *Campylommata bilineata*. In 1898 Jameson observed the mice on an island in Dublin Bay and found that owls and hawks on the island eliminated the darker coloured forms quicker than the lighter coloured forms. These latter types resembled the sandy background and they had a natural advantage. They were in great excess in the population. Weldon¹ claimed to show that shore crabs (*Carcinus matthes*) in Plymouth Sound which possessed a narrow carapace were selected against those with a wider carapace. In 1899 also, Bumpus found that English sparrows in America possessing certain structural features were selected by strong winds against those sparrows lacking those structural features. In 1911 Harris submitted Bumpus' work to a statistical analysis and confirmed his conclusion. Also in 1899 Poulton and Saunders exposed the pupae of *Vanessa urticae* on different contrastingly coloured backgrounds and found a selective elimination by birds. Crampton² made a very comprehensive study of over-wintering pupae of *Philesomia gynostia*. He collected large numbers of cocoons and examined them to see if they were alive or dead. By means of measurements he showed that fitness to survive was dependent upon a proper co-ordination of structural and functional characters. Davenport in 1908 found a differential elimination of black and white chickens by crows among flocks consisting of black, white and pencilled birds. Finally Thompson, Bell and Pearson in 1911 found selection of a race of wasp (*Vespa vulgaris*), while in 1915 Lutz estimated the survival value of some structural features of *Drosophila* after starving them during their embryonic development.

(b) *Later direct observations and experiments*

Heslop Harrison³ found evidence of changes in populations and of the effect of selection on local races of *Operabia autumnata*. This moth ranged over the whole of Eston Moor in the Cleveland district of Yorkshire apparently from the Middle Ages up to 1860 by which time the area had been split up into eastern and

¹ 1899.

² 1904.

³ 1920.

western plantation areas separated by a half-mile belt of bracken and heather. The moths were confined to the woods because of their feeding habits. Originally both woods had been coniferous with a little birch and alder. But in the course of time a gale had destroyed the trees in the western wood and the conifers became largely replaced by birch. Harrison found that there was a definite selective elimination of lighter coloured forms of *Oporinia* in the dark coniferous wood even when the proportion of dark to light coloured forms was as high as 25 : 1. The predators were identified as bats and owls which selected the light coloured moths resting on the dark trees during the night.

A thorough investigation was carried out by Quayle¹ and other workers in the field and in the laboratory on the genetics, physiology and distribution of resistance in types of scale insects. These *Coccoidea*, or scale insects, ravage the citrus groves on the western seaboard of America. Hydrocyanic acid sprays are generally used against these pests, but in 1914 Melander produced evidence showing that immunity to this poison was developing in the insects, and in the same year Quayle found that the red scale (*Aonidiella aurantia*) was still abundant after spraying with hydrocyanic acid in some orchards in California, while in nearby orchards spraying had been successful. By 1937 the resistance had persisted and had spread to more outlying districts. Then Quayle² and Lindgren³ and others began systematic work on the insects. Two types of red scale were found—a resistant and a non-resistant race. Over four generations this difference in resistance was maintained. Insects resistant to hydrocyanic acid were also relatively more resistant to other insecticides. Indications were that the resistance was due to some genetic factor and indeed Dickson⁴ showed in 1940 that the hybrid between a cross of resistant by non-resistant was intermediate with respect to the condition and resistance was controlled by a sex-linked factor. Quayle also found another scale insect which developed a resistant type and the latter spread to neighbouring groves very rapidly. Other workers have studied other local resistant races which arose spontaneously.⁵ It is considered that these resistant races were enabled to spread by selection which eliminated the non-resistant

¹ 1938.² 1938.³ 1938.⁴ 1940.

⁵ See Woglum, 1925, on the black scale (*Saissetia oleae*) and Gray and Kirkpatrick, 1929a and b, on the citrus scale (*Coccus pseudopalmarum*).

insects. It seems probable that these insects spread from an original focal area.

A somewhat similar story concerns the Codling Moth (*Carposina pomonella*), a serious pest of apple and pear trees in Colorado and Virginia. This insect seemed not only to show an increased resistance to the usual sprays but was also spreading to walnut trees.¹

A very neat example of the action of selection was given by Sheppard, and Cain and Sheppard, using the snail *Cepaea nemoralis*.² This snail is phenotypically polymorphic, existing in forms which are variously banded; these forms have existed since Neolithic times³, thus indicating that the banded patterns have survival value. Other biologists, however, have thought that the patterns are relatively neutral.⁴ Cain and Sheppard,⁵ by examining random samples from many populations of the snails, found that there was a greater preponderance of yellow-banded snails on greener backgrounds, and on the more uniform backgrounds the number of effectively banded shells was much lower. When the snails were studied on the basis of their environment it was found that those in similar environments resembled each other more than snails from dissimilar habitats and the variation in the patterns was greatest the greater the variation of the background. These observations suggested that certain types of snails were being selected on certain backgrounds and indeed this was proved to be the case when, later, Sheppard, using marked shells, and by examining thrush ' anvils' (i.e., the stones against which the birds crush the snails to break the shells), found that the Song Thrush (*Turdus sericiformis*) in fact killed greater numbers of yellow coloured snails on a brown background and more pink and brown ones on a green background.⁶

While collecting insects from ponds Popham⁷ noticed that the colour of most species of the Water Boatman matched that of their background. By measuring the colour variation of the insects and of the background, using a standard Ostwald colour chart, he showed that the species of Water Boatman were at ease on a background of the same, or similar, colour to themselves, but were restless and attempted to fly away on a differently coloured back-

¹ See Hough, 1934, and Smith, 1941.

² Sheppard, 1931, 1932, 1934; Cain and Sheppard, 1930.

³ See Diver, 1929. ⁴ See Mayr, 1942. ⁵ 1930.

⁶ Sheppard, 1931, 1932 and 1934. ⁷ 1941.

ground. In his experiments he used large tanks filled with water to a fixed depth; the bottom of the tanks was covered with mixtures of cement, sand and emery to give a series of definite colour values. The insect used was *Arctocoris distincta* and the predator was the Rudd (*Lencisens erythrophthalmus*). In various combinations of coloured backgrounds and insects it was found that insects with a colour value resembling that of the background were protected. Popham also varied the light intensity and found that this affected the power of the Rudd to discriminate between the insects. Similar results were obtained when the number of insects were decreased or the number of predators was increased. In mixed sizes of insects the Rudd chose the intermediate sizes. Popham concluded from these elaborate experiments that adaptive coloration of the insect has a certain selective value but selection was not the only factor at work.

Some more or less direct account of changes in whole populations over a period of years have been published. It is inferred from these observations that selection is the agent responsible for the changes. For example, the melanic (black) form of the peppered moth (*Amphidays betularia*) was first found near Manchester in 1850, but now it has supplanted the original non-melanic form in many places. The diurnal butterfly *Heodes philes* L. has a very wide distribution over most of the northern hemisphere, but the variety from Madeira shows little affinity with those from other areas. Ford¹ examined the collections made by Wollaston, and, on comparing them with his own collections caught about seventy or eighty years later, found that there were slight but definite differences in the populations. Ford² also described an interesting example of variation of a population of the Marsh Fritillary (*Euphydryas aurinia*). We quote the relevant paragraph:

The species was quite common in 1881, and gradually increased until by 1894 it had become exceedingly abundant. After 1897 the numbers began to decline, and from 1906 to 1912 it was quite scarce. From 1913 to 1919 it was very rare, so that a few specimens only could be caught each year as a result of long-continued search, where once they were to be seen in thousands. From 1920 to 1926 the butterfly had become excessively common, and so it remained until we ceased our observations in 1935.

¹ 1923-24. ² 1945, pp. 268-269.

When the population was small variation was low and the population consisted practically of a constant form; when the population was large variation was extreme. Ford inferred that the environment determines the size of the population and that, in consequence, when it was small selection would be intense and variation would be at a minimum; but when the population was large and the environment favourable selection would be weak allowing for much variation.

We have already mentioned the Black Peppered Moth, and in general, industrial melanism in insects furnishes good examples of changes in population over a period of years. The changes are apparently brought about by the selective elimination of one type, or the preferential selection of a new type in relation to the habitat. In general the darker coloured varieties are favoured against the lighter coloured varieties, especially in industrial areas. There are many examples of the spread of industrial melanics and good accounts were given by Ford¹ and Hesbrook.² Ford also found that the melanic forms were often more robust than the lighter coloured types and indeed Heslop Harrison in 1920 had already noticed this feature.

It is scarcely possible to examine wild colonies of bacteria directly; they must always be grown in the laboratory for sustained examination. It is doubtless true that in the case of such organisms comprehensive culture experiments give an indication of the effect of selection as it exists in nature. In 1930 Todd reported the effects of selection on *Streptococcus haemolyticus*, the cause of puerperal fever and scarlet fever. When this bacterium was grown on agar (a prepared jelly obtained from seaweed) it soon lost its virulence and infectibility. Todd found that it produced hydrogen peroxide and in culture this substance was toxic to it. Mutations, however, arose which did not produce this hydrogen peroxide, or at least formed much less of it compared with the normal strain. Hence the mutants could live in the culture medium but they were less virulent.

Recently K. C. Atwood *et al.*³ made a long-term population study of the bacterium *Escherichia coli* in which the experimental cultures were allowed to grow for periods varying between a few weeks to six months. They found a series of mutations which had

¹ 1937. ² 1934.

³ K. C. Atwood, L. J. Schneider, and E. J. Ryan, 1951.

small differences in adaptive value. When these mutants were allowed to exist in a population the latter became replaced by a new one consisting of the mutant types. The type of selection involved here is called *periodic selection* because it acts in the same way as a periodic artificial selection would act by isolating a few bacterial cells at intervals in order to start new populations. The selection is further non-specific, that is, it simultaneously alters the frequencies in a population of a number of unrelated mutations. Hence, as the population ages, all mutants except the small adaptive ones will be eliminated and the population will have changed. But the process is reversible by means of an alteration in the environment. As we have already mentioned, in 1928 F. Griffith discovered that a transformation (or 'mutation') could be induced in unencapsulated pneumococci by addition of extract of an encapsulated form to the medium in which the former was growing. Since then other transformations in various bacteria have been described. Study of these changes shows that different ones were selected in different environments. A detailed account of these changes was given by White, Robinson and Barnes¹ and Dobzhansky.²

c) *Modern indirect observations*

While the direct quantitative experiments showing the occurrence of selection are few in number, there is an increasing number of indirect laboratory or garden experiments of many different kinds. It is important to know of these in order to appreciate the dimensions and comprehensiveness of the selection process, and to form an opinion of its value in nature and in evolution. A selection of these experiments is given below.

A number of well planned and informative examples of the action of selection in closely related but sharply delimited varieties of plants have been given since Turesson³ introduced the term *ecotype*. The chief contributors to this work have been Turesson³ in Sweden, Turtill and his colleagues⁴ in England, Gregor⁵ in England, Clausen, Keck and Hiesey⁶ in America, Sukatschew⁷ in Russia and many other botanists.

Well-marked varieties, particularly of plants, often grow in distinct habitats. Sometimes they are confined to a particular

¹ 1938. ² 1931. ³ 1912, 1925, 1926, 1929, 1930.

⁴ 1938a and b. ⁵ 1930, 1931, 1933, 1939; & Gregor *et al.*, 1936.

⁶ 1934 and series of Year Books, Cam. Inst., Wash. ⁷ 1928.

habitat. Turesson transferred several forms of this kind to his garden and found that they bred true to their special diagnostic morphological feature. He called such forms *ecotypes*. Many species are found to possess several ecotypes and apparently they enable the species to adapt itself to local environmental conditions. If the environment changes, some ecotypes may be selected against, so that a change in the frequencies of occurrences of the ecotypes is produced, and in this way a population may be altered in composition. Experiments of this kind which involve transferring plants from the wild to experimental plots are called transplant experiments. The plants are then studied at all stages of growth and much information is given. For example Turrill¹ summed up some of the results of Marsden-Jones and Turrill² and found that over a ten-year period 'Every species reacts differently from every other, though a classification of reactions is possible if any class is diagnosed by a certain range of behaviour. Thus, to take a few examples, *Centaura nemoralis* survives well on all soils but shows little morphological change on any; *Plantago major* L. very quickly reacts to the different soils by most conspicuous changes in size, number, orientation, etc., of vegetative and reproductive organs; *Polygonum nodosum* and *P. pratense* show, on the five soils, slowly marked quantitative differences, but these are more slowly cumulative; several species show differential death rates, with or without structural changes. The greatest and most rapid changes have been recorded for *Plantago major* L., an extremely plastic species. Here, phenotypes have been produced within two years, from seedlings and from ramets³ of a single clone,⁴ which have been classed as varieties and sub-species in a recent monograph of the genus.'

Sukatschew⁴ studied the dandelion (*Taraxacum officinale*) by taking three individual plants from a field. From these plants three clones,³ A, B, and C respectively, were obtained which could be morphologically distinguished. These strains and their descendants were then dealt with on experimental plots, and the seedlings were planted in two different densities, viz., a lower density of 10 cms. and a higher density of 30 cms. between each seedling. The plants were allowed to grow for two years and then

¹ 1940. ² 1938; 1928-1938; 1930-1938.

³ Ramet in higher plants is an individual belonging to a stem which is a group of individuals of independent organisms derived vegetatively from a common ancestor.

⁴ 1928.

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the number of the surviving types was counted. The results are given below. At the same time plots were set up of all three clones mixed together and the results recorded after two years. These results are given in brackets below.

Percentage number of plants lost			
Density	Clone A	Clone B	Clone C
Low	22.9 (16.5)	31.1 (22.1)	10.3 (5.5)
High	73.2 (72.4)	51.2 (77.6)	75.9 (42.8)

In the single strains those at a low density in clone C survived best, while at a high density those of clone B were most viable. In the mixed groups those in clone C were much more viable than those in either clones A or B. He carried out other similar experiments with varieties from different regions of Russia and obtained similar results showing that differences in viability depended to a large extent on the environmental conditions under which the plants were growing.

As an example of Turesson's work we may mention his study of the alpine ecotypes of *Solidago virgaurea*,¹ or his work with *Hieracium umbellatum*.² In the latter case there were two ecotypes of *Hieracium*, one growing only on sand-dunes and the other only on sea-cliffs. These habitats alternate on the southern coasts of Sweden, as do the ecotypes.

Some observations have also been made on insect populations. For instance, Timofejeff-Ressovsky³ cultured samples of *Drosophila melanogaster* with various geographical races of *D. funebris* and found that the survival value of the former was higher than that of the latter; the races of *funebris* differed in survival value among themselves. There are two races of *Drosophila pseudo-obscura*, Race A which inhabits regions with a hot summer and Race B which prefers more temperate regions. Race A lays more eggs at a high temperature than Race B and at a lower temperature Race B lays more than Race A.⁴ Reed and Reed⁵ and Merell⁶ worked on problems of selection between the wild type red-eyed *Drosophila* and the white-eyed mutant. They found that, in mixed cultures of the flies, both the red and white females chose red-eyed males as

¹ 1933 and 1935.

² 1925, 1931.

³ Dobzhansky, 1935.

⁴ 1950.

⁵ 1933.

mates as against the white-eyed males which were thus selected against. L'Heritié and Teissier¹ cultured mixtures of various types of *Drosophila* mutants in known proportions. They found that in a mixture of normal winged and vestigial winged flies exposed to the influence of the wind, the proportion of the vestigial flies increased, but in a mixture of normal and bar-eye mutants the proportion of the latter decreased. Also in a mixed population of normal, ebony mutants and the hybrids between them, the hybrid showed a selective advantage. Finally, Spencer² found that under normal conditions the vestigial mutant of *Drosophila* was less viable than the normal fly, but when food and water were scarce the viability of these flies was increased.

The topics of mimicry and protective coloration in animals should rightly be considered at this point. Under both of these subjects there are plenty of good examples of the action of selection among organisms. The subjects, however, are large and cannot be shortly summarized. For fuller information of them the reader is referred to H. B. Cott's *Adaptive Coloration in Animals*.³ One or two illustrations from among many will be mentioned here. Many animals require to protect themselves from the ravages of predators if they are to survive. And the animals do this in many different ways, which may be summed up under the headings of mimicry and protective coloration. As Cott⁴ said: 'Innumerable animals, inhabiting all kinds of surroundings, tend to wear on their bodies a cryptic dress.' They do this by means of a host of colourings and elaborate patterns on their bodies or on their wings if they are insects. Thus the appearance of the animal comes to resemble the background on which it lives and predators find it difficult to distinguish between the animal and the background. Often those that are out of place as it were will be selected against and thus destroyed. Thus in nature animals which are protected by some means of this kind show a lower death rate compared with those which are unprotected. There is a differential death rate between protected and unprotected animals. In mimicry an animal seems to copy the pattern or colour of an animal which is already protected by reason of its pattern or colour. Sometimes inanimate objects are mimicked. Famous examples of these forms are the various stick insects which resemble sticks and those which resemble leaves.

¹ 1934 and 1937.

² 1932.

³ 1940.

Animals in general do not eat indiscriminately but choose their food with care, and so experiments on selection with regard to prey and predator may be made. These are direct evidence of selection in showing that an animal will choose some favourable conspicuous living morsel of food. If such animals are difficult to discern on the background a differential survival rate is set up in the populations. Well-known experiments were given by Sumner,¹ Cesnola,² Beljajeff,³ Carrick,⁴ Young,⁵ Gerould,⁶ Isely⁷ and others. Only one of the earlier experiments will be given as an illustration. It is chosen because the results are clear although the numbers involved do not admit of statistical analysis.⁸ Cesnola⁹ worked with the praying mantis (*Mantis religiosa*) in two forms, a green one and a brown one. In nature the green form always occurs on green grass, while the brown one lives on sun-scorched grass. Cesnola collected 45 green and 65 brown specimens and tied them to individual plants by means of silk threads. Thus, 20 green insects were tied to green plants with green herbage; 25 green were tied to brown plants covered with burnt brown herbage; 20 brown were tied to brown plants on a brown background and 45 brown were tied to green plants on a green background. Cesnola found that after eighteen days the protected insects (that is, those whose colour resembled the plant and background) had all survived, while all the green insects on a brown background had been killed after eleven days and only 10 of the 45 brown insects on a green background had survived. Then the wind blew the remainder away. The predators were ants and birds. Cesnola's results clearly illustrate that protective coloration has a selective value.

C. Selection, population studies; homeostasis and speciation

We have now discussed some features of selection in evolutionary theory. Selection must always be in operation whether evolution occurs or not (evolution and selection are not synonymous). At the lowest level selection implies the direct elimination of the unfit. On the basis of the factors of evolution, i.e., mutation, recombination, isolation and selection, the mathematical selectionists have built up a marvellous superstructure

¹ 1934, 1935a and b.

² 1904.

³ 1927.

⁴ 1936.

⁵ 1936.

⁶ 1936.

⁷ See also Petherill, 1951, for a short general account.

⁸ 1936.

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which has led to a great understanding of the mechanisms of microevolution, or evolution on a small scale or at a simple level, sufficient for biologists to assert that they know what evolution is at this level, but also sufficient for them to realize that there are great unplumbed depths awaiting investigation. Evolutionists owe a great debt to these mathematicians, to R. A. Fisher, Sewall Wright, J. B. S. Haldane, K. Mather, H. Muller and others who have made this position possible. But we should also remember that the mathematical models are only models, and mathematics is not biology and can never be substituted for it. These mathematical models are admittedly oversimplifications of the true picture which is plainly very complex in nature, perhaps too complex for complete analysis, but they represent abstract statistical generalizations of how evolution may have occurred under given conditions. As P. M. Sheppard¹ said:

Our knowledge of the theory of evolution is now extensive, chiefly as the result of the mathematical approach to the problems adapted by Fisher, Wright, Haldane and others. However, of necessity much of the work is based on assumptions about population structure and selective intensity which has not yet been adequately investigated in the wild.

Some observational work, however, has been done on wild populations which have been examined in nature and in the laboratory. While this work is not as yet extensive it has indicated some important points. Naturally-occurring mutations similar to those found under experimentally controlled conditions have been identified. Much of the work along these lines was done by H. A. and N. W. Timofeeff-Ressovsky,² Tschetvrikov,³ Dubinin *et al.*,⁴ Gershenson,⁵ Gordon⁶ and others in various parts of the world, and the organism involved was *Drosophila*. When *Drosophila* flies from wild populations were bred in the laboratory in such a way that recessives could be extracted, it was found that the differences between the various races were gene differences affecting quantitative characters, and they were similar to many of the mutations arising in old cultures of the flies. Different populations were found to contain different concentrations of mutations; some populations contained similar mutations, others

¹ 1953 ² 1927. ³ 1928. ⁴ 1934, 1936 and 1937.

⁵ 1934 ⁶ 1935.

different ones. These mutations were largely present in the populations as heterozygotes. Similar investigations and results were obtained by Sexton and Clark,¹ who studied populations of a crustacean, *Gammarus chevreuxi*. It seemed then that the material for evolution was present in natural populations. Since then more evidence has become available to support this conclusion, but it may be said that it concerns small mutations leading to micro-evolution. It has not been demonstrated that an accumulation of small mutations leads to macroevolutionary effects, although it is theoretically possible, and even likely, and there is evidence suggesting it.

A species is a component structure, and its parts may be at different evolutionary levels, hence the mechanism of evolution may vary accordingly. In Darwin's day it was taken for granted that evolution implied the multiplication of species, but this is not necessarily so. A species may change in the course of time to produce another species which may supplant the first one, and this process may be continuous. Thus it is possible for evolution to proceed at the level of the gene, of groups of genes, of the chromosome, of the whole set of chromosomes in an individual, of the race, of the population and of the species. Changes within individuals lead to variations in a group, but these variations occupy a definite *milieu*, or more than one *milieu*, and are subject to the forces at work therein which often have a selective effect. In a sense variation is positive and selection is negative, but, as Clausen² found, these two oppositional forces are always in a state of dynamic equilibrium and as a result the species possesses a reserve of variability and a power of adaptability which renders evolution possible.

The taxonomist recognizes a species as a group of organisms possessing a definite combination of morphological characters, and hence in classification the limits of the species are often seen to be tenuous. The existence and the origin of such species enters into the consideration of evolutionists, of course, but the taxonomic or systematic species is not very suitable material for genetic analysis unless it is clearly defined. Mayr³ defined a species as follows: 'Species are groups of actually or potentially interbreeding natural populations that are reproductively isolated from other such groups.' This natural or ecological population is,

¹ 1936.

² 1954.

³ 1949.

however, still not definite enough for the geneticist. He recognizes what is called a *Mendelian population* which is a genetical population based on the genetic make-up and breeding behaviour of the organisms comprising it. Dobzhansky¹ defined it as 'a reproductive community of several and cross-fertilizing individuals which share in a common gene pool'. He pointed out that the largest and most inclusive Mendelian population is the biological species. These may be divided into sub-species, races or local populations, according to whether they have common gene pools. The race may inhabit several islands in an archipelago, but it would not necessarily form a common Mendelian population because of the genetic isolation and differences. In modern genetical evolutionary theory populations are coming to be considered as the evolutionary unit. It is the population that evolves and, in general, it is continually changing because of the heterogeneous gene pools of its members. The various chromosomal and genetic conditions allowed free play in a population are continually producing new combinations. Selection acts on the phenotype of the individual and thus new combinations of the gene pool which alter the genotype will also be subject to a selection pressure. As Clausen² said:

The myriads of existing and potential biotypes of each local population are in dynamic balance with each other and are balanced against the forces of the environment which change from hour to hour, from day to night, from season to season, and from year to year. The gene systems that determine the expression of the characters of natural races of plants are themselves composed of genes of oppositional, accumulative, subtracting and complementary effects; such an arrangement makes a greater range of potential variability possible than would a supply of genes merely working in one direction.

The criterion for survival in a population is *adaptedness*, but different individuals may have different degrees of adaptedness. The criterion for survival of a population is *fitness*, by which is meant that the population must maintain itself in the environment and be able to use any variability in its gene pool to extend its adaptability if the environment changes. Individuals also may be fit in this sense, and the fitness of individuals and the population

¹ 1950. ² 1954, p. 476.

must obviously be related. In fact, Mendelian populations have an integrated structure which facilitates evolution at all levels but under the influence of selection. Investigation has shown that there are many recessive alleles in *Drosophila* populations—the gene pool consists of mixtures of all sorts of genetic and chromosomal arrangements. But the population is still successful under selection; in other words, the population shows balanced polymorphism of different genotypes. In such populations heterozygotes seem to be better adapted than homozygotes and show *heterosis* (which here means increased fitness). There are a few observations which indicate that heterozygosity has a selective advantage over homozygosity in populations. For example, A. Buzzati-Traverso¹ found that in flies of *Drosophila subobscura* heterozygotic inversions were necessary; while Dobzhansky *et al.*² found that flies heterozygous for certain chromosome inversions had a selective advantage over homozygotes. And again, Stern *et al.*³ even showed that lethals may have a selective advantage in the heterozygous state. And there are other examples.

To illustrate balanced polymorphism we may take the simplest case given by Dobzhansky.⁴ We quote his words.

If two gene alleles or chromosomal variants, A^1 and A^2 , form a heterozygote, A^1A^2 , which is adaptedly superior to both homozygotes, A^1A^1 and A^2A^2 , natural selection will tend to establish an equilibrium state at which both A^1 and A^2 will be present with certain definite frequencies. The crux of the matter is that the *average fitness of an individual in the population* will be greatest when A^1 and A^2 reach equilibrium frequencies. In other words, natural selection enhances the adaptedness of the Mendelian population as a whole, at the price of continuous production of some less well adapted individuals.

This is a very important theoretical conclusion which Dobzhansky elsewhere⁵ pointed out needs experimental verification involving measuring the actual fitness of a population compared with other populations. A fit population is composed of fit and unfit, or perhaps it is better to say fit and fitter, individuals, but the fitness, or survival value, of the population depends, not on the fitness of the individual, but on the population as a whole. Without

¹ 1951. ² 1951. ³ 1952.
⁴ 1950, p. 410. ⁵ 1955.

the initial presence of the less fit alleles A^1 and A^2 , the fitter heterozygote, A^1A^2 , could never have arisen.

J. M. Thoday¹ considered that fitness for survival comprises a unit of evolution, and the fitness of such a unit is 'its probability of leaving descendants after a given long time' (such as, say, 10^3 years). Increase in such fitness comprises biological progress. Thoday² stated the components of fitness to be (a) adaptation, (b) genetic stability, (c) variability which includes genetic and phenotypic flexibility, (d) the stability of the environment. Within a population or species these components will normally be balanced.

Thus the essential feature in evolutionary genetics is to determine the fitness of the population in relation to an evolutionary time scale. In practice this means finding out how a population becomes adapted to the environment, and even more to several environments. Dobzhansky and Wallace,³ and others, have indicated that a maximum of adaptability may be attained (a) in balanced polymorphism as already indicated, because then the population consists of a large number of different genotypes each of which may be specifically adapted to a specific part of the large environment, and (b) by an adaptability which will allow individuals in the population to adapt to a spreading environment. Such adaptability leads on to genetic homeostasis which is connected to fitness in populations. The subject of genetic homeostasis is new, and even the basic ideas are not yet sorted out, but we may give an outline of what it means from an evolutionary point of view. Essentially homeostasis seeks to find an explanation of ability to adapt to several environments. Lerner⁴ stated: 'Homeostasis refers to the *prospects* of an organism to adjust itself to variable conditions, or to the self-regulatory mechanisms of the organism which permit it to stabilize itself in fluctuating inner and outer environments.' The word derives from an original physiological meaning given to it by W. B. Cannon.⁵ The idea that homeostasis of individuals is important in evolution was first advanced by H. J. Muller⁶ and C. H. Waddington.⁷ Lerner⁴ developed the thesis that Mendelian populations possess self-regulatory properties, and that there is a connection

¹ 1953.

² 1953.

³ 1950.

⁴ 1953, p. 112.

⁵ 1932.

⁶ 1948.

between genetic and developmental homeostasis, while heterozygosity gives a basis for these phenomena.

When a new allele or mutation appears in a population several things may happen to it, depending on the degree of expression in the phenotype and its response to selection. If it is dominant and deleterious, it will be quickly eliminated, but if it is recessive and disadvantageous it may remain dormant in the population in a low frequency; but if it is a favourable and dominant allele it will replace the wild type allele to some extent, while if it is favourable and recessive it will replace the wild type completely. These conditions are brought about by selection pressure acting on the gene mutation which will set the frequency of its occurrence. Lerner¹ summed up his conclusions in the following words:

Each genotypic combination may well represent a unique constellation of genes. It is impossible to predict its competitive value under uncontrolled conditions. Nature depends on trial and error and hence needs a wide base of genotypes on which to operate. Error is minimized in successful populations by developmental homeostasis. Genetic homeostasis arises as an after-effect. But the perpetuation of Mendelian populations, whether in nature or under man's control, remains a stochastic² process. The purpose of research in population genetics is to gain a better understanding of evolution, which is another way of saying that we seek to narrow the confidence limits of prediction regarding the fate of any population.

Heterozygosity is thus of great importance, and Lerner considered that heterozygotes possess a selective advantage over homozygotes because of a more balanced phenotype which they produce.

Lewontin³ extended Lerner's meaning of homeostasis to enable comparisons between genotypes to be better attempted. He considered that a genotype is homeostatic when individuals within it are able to adjust their morphogenesis and physiology so as to survive and leave offspring in a large range of environments. A population or species is homeostatic when either its genotypic or its phenotypic content is suited to a variety of environments. Hence homeostasis has a two-fold aspect—part of its mechanism keeps the basic physiological and morphogenetic processes of the

¹ 1954, p. 120.

² Stochastic = to aim at a mark, guess pertaining to conjecture (*Oxford Dict.*).

³ 1956.

organism constant, and the other part allows for ability for adaptive adjustment to varying conditions of the environments. If the constant feature in homeostasis was not present a population might, under the action of an intense unidirectional selective force which became non-adaptive, lead to an evolutionary dead-end. On the other hand, a complete constancy resisting change could also be non-adaptive, leading to extinction. Homeostasis maintains the balance and allows for progressive evolution. As Thoday¹ pointed out, any population which is going to evolve genetically must be heterozygous in order to maintain variance, and the cardinal feature of heterozygosity is that it allows segregation leading to outbreeding and heterozygotic balance. This balance maintains the outbreeding and results in genetic homeostasis.

In Mendelian populations there is a spread of genotypes which, as they are members of a common pool, are related. Dobzhansky² called this spread of genotypes the 'adaptive norm' of the population. The adaptive norm sums up the evolutionary history of the population, and, while it is an abstraction, its consideration leads to understanding of population genetics and their evolution. The origin of adaptive norms may be studied under two main hypotheses which are not mutually exclusive. Dobzhansky gave these as follows. The first is the *classical hypothesis* whereby favourable gene and chromosome structures supplant the unfavourable gene and chromosome arrangements. In a population where this process is occurring, the individuals will tend to become homozygous for the majority of genes, thus reducing the actual number of genotypes. Genetically such a population would be neutral, transient or morbid. The second is the *balance hypothesis* in which the situation is completely different. Here the adaptive norm consists of a large number of different genotypes heterozygous for many genes. In such a population heterozygosity might become obligate. Selection will favour the increase of heterozygosity, that is, the production of many different alleles leading to a greater variety of genotypes. Hence, by reduction of the number of homozygotes a greater adaptedness of the population would be produced. A relational balance would be set up between the genotypes which would then act like an organized system, and acquire genetic homeostasis.³

¹ 1935.

² 1935.

³ Dobzhansky, 1935, p. 3.

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A selective advantage of heterozygosity is that it increases the adaptiveness of a population, because, due to recombinations, a variety of phenotypes may be produced which will suit various ecological niches in the environment—that is, small local areas with specialized local conditions as compared with the larger general environment of the population as a whole. If there is an intensive selective effect in such ecological niches homozygosis may increase in amount. If the organisms being favourably selected in the niches become partially genetically isolated, or isolated in some other way, and selection remains constant internally and externally, local races will be established which will then tend to diverge or evolve separately. It is generally recognized nowadays that evolution will proceed relatively rapidly when a population, or a species, is separated into distinct breeding units in such ecological niches, or localized regions. R. A. Fisher and E. B. Ford¹ considered that selection alone will determine the various genotypes thriving in such niches, that is, that fluctuations of all gene frequencies in a large population is due to selection. Once established the alleles of the variants may become dominant to the original wild type genes of the population as a whole; changes may occur by mutations and the local population may begin to spread back to the original larger population which will now be acted on by the dominant alleles.

We may now mention again Sewall Wright's conception of *genetic drift*, or the *Sewall Wright effect*.² Drift is an error of sampling occurring in a large population as a result of the splitting up into smaller populations in ecological or other niches with special local conditions. Wright¹ also pointed out the probabilities of change in various populations, as follows. In very small local populations there is very little variation, or selection, and the variants in the population become static. Mutations may occur, but these mostly lead to degeneration and ultimate extinction. In very large populations in which free interbreeding occurs there is a great deal of variability, but the gene frequencies are in approximate equilibrium, and hence there is little evolution. A change in conditions, such as a change in the selective pressure, moves all the gene frequencies to a new equilibrium for as long as the new selective pressure exerts its effect. Evolution does occur in such large populations, but it is a very slow process. In a

¹ 1947.

² 1931, 1932, 1933, 1940.

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population intermediate in size between the very large and the very small there is a constantly occurring and random movement of gene frequencies while selection is altering likewise; hence there results a relatively rapid, continuous and irreversible series of changes which are not degenerative. This process will take place even under static conditions. Even so, periods of about 100,000 generations will be required for important changes to occur in the population.

Wright then proceeded to state the effect of random drift as follows:

Finally in a large population, divided and sub-divided into partially isolated local races of small size, there is a continually shifting differentiation among the latter (intensified by local differences in selection but occurring under uniform and static conditions) which inevitably brings about an indefinitely continuing, irreversible, adaptive and much more rapid evolution of the species (than in a comparably large, random breeding population).

Thus there is some disagreement about the selective importance of the factors bringing about evolution of these local populations. Ford and Fisher (as already mentioned) and others considered that selection alone is the deciding factor. Wright, on the other hand, considered that fluctuations of gene frequencies in a large population may be due to random genetic drift, or to selection, or to both, operating together. Wright has always maintained that evolution is the result of the operation of a balance between all the factors taking part in the process. Sheppard,¹ after reviewing the situation, concluded that selection is the predominant agent in evolution and that Wright's genetic drift 'is of negligible significance as compared with selection'.

In order to resolve this situation it is probably necessary to find out how genes or genetic changes move in a population. Not a great amount of work has been done on this particular problem, but we may cite an elaborate and beautiful study by R. A. Fisher and E. B. Ford, and one by Dobzhansky. Fisher and Ford² studied the frequency of occurrence of a variant of the moth called *Panaxia dominula* L. A variety called *medionigra* is a heterozygote for the normal gene affecting a central yellow wing spot and other features. It behaves as an allele to the wild type gene in the normal

¹ 1934. ² 1943.

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or commoner form, *P. dominula*, and in the homozygote *P. bimacula* Cockayne. In a study of a colony occurring near Dry Sandford, Berkshire, spread over eight years, Fisher and Ford found that prior to 1929 the frequency of the *medianigra* gene in the colony was about 1.2 per cent. By 1939 it had increased to 9.2 per cent and in 1940 it reached its highest frequency of 11.1 per cent. Thereafter from 1941 to 1946 its frequency was 6.8, 5.4, 5.6, 4.5, 6.5 and 4.3 per cent respectively. The mean value is therefore 5.2 per cent throughout these years and there is no indication that the frequency was reverting either to the low 1.2 per cent or to the high 11.1 per cent. Fisher and Ford found that random survival could not account for such fluctuations in frequency, which must be due to selection. They do not think, however, that such changes in gene ratios in very small populations have much evolutionary significance. Dobzhansky,¹ investigating a natural population of *Drosophila pseudo-obscura* in California between 1939 and 1946, found that the relative frequency of the Standard gene arrangement on the third chromosome increased significantly at the expense of the Arrowhead and Chiricahua arrangements which was probably caused by natural selection, but this was not certain.

3. POLYGENIC INHERITANCE²

The idea of polygenic inheritance is receiving an increasing amount of attention because it is aiding selectionists to find a workable basis for Darwin's original idea that evolution proceeds by means of the accumulation of small advantageous variations. There is now a fairly large literature on the subject and its applications, but the basic ideas behind it are simple. The reader will find an excellent review and more detail in a paper by K. Mather³ which states the position clearly. Since then further confirmations and developments have been put forward.

The theory of polygenic inheritance springs directly from the statistical study of variation in organisms. In ordinary genetics relatively large phenotypic variations (such as, say, red flower colour or white flower colour) are mostly studied because they are easy to observe. Often these differences are under the control of alleles of a wild type gene and they behave in inheritance in the

¹ 1947. ² See also pp. 139-190. ³ 1943 and later 1953.

known Mendelian manner. This type of variation is said to be *oligogenic*. However, observation of a group, or population, of different species, or different varieties of species, invariably shows many characters which are not so clear cut as red and white in flowers; for example, consider merely the question of height, or weight, in human beings. Characters of this kind vary quantitatively, and they are often called quantitative characters. If such characters are expressed in a graph they give a normal curve of variation with two extremes at the bottom of both ends of the curve and the mean, or average, value in the highest centre part of the curve. There is a good deal of evidence for the statement which Mather¹ gave regarding these characters. He said:

A second type of heritable difference shown by species is dependent on the joint action of many genes, each having an effect small in relation to the total non-heritable fluctuations of the character in question. Such differences are termed polygenic and polygenic characters do not show sharp segregation. They may exhibit any degree of expression between wide limits and hence have often been called quantitative characters. . . . Polygenes are inherited in exactly the same way as other genes, in that they are situated on the chromosomes.²

Polygenes individually produce so small a phenotypic effect that they are masked by the ordinary fluctuating variations due to the environment. Darlington³ called them the 'invisible genes'.

It seems to be impossible at present, however, to study individual polygenes, but they are known to segregate and recombine and form linkage groups in the same way as ordinary genes. Chromosome maps of polygenes may also be constructed; for example, L. G. Wigan⁴ obtained a rough map for the polygenes on the X-chromosome of *Drosophila melanogaster* which control the number of sternopleural bristles.⁵

Thus polygenes are composite and are best considered as a whole, or as a system. They are always balanced in their effect on the phenotype, but individual polygenes may mutate. Due to crossing-over frequent genetic recombinations of these genes will occur producing small phenotypic variations which will sooner or later come under the influence of selection. As their individual

¹ 1943, p. 35.
⁴ 1949.

² See also Mather, 1942, and Warren, 1924.

³ 1953.

⁵ See also Mather, 1949a, and b; Mather and Harrison, 1949.

effect on the organism is very small, the many combinations of them in a single gene pool, each one genetically distinct, produces a graded variation phenotypically. As Mather said in general, 'Polygenic theory relates continuous phenotypical variation to discontinuous genotypical variation, the biometrical to the genetical.' It was always a puzzle to the older Darwinians and their critics how continuous variation could be explained by relatively large mutable discontinuous genes. Polygenic inheritance may provide the answer and in a sense it thus connects what used to be called 'blending inheritance' with Mendelian genetics. The existence of polygenes gives great support to Wright and Fisher's theories of selection as a determining factor in evolution. As related species, particularly of *Drosophila*, often show polygenic variations it is considered by many geneticists that speciation is probably due to a gradual accumulation of many small genetic variations of the polygenic type. This has led Mather to consider that macroevolution at the species level differs only from microevolution, or evolution within the species, in quantity of change and not in essential nature. The difference would be one of degree, not of kind. These, however, are speculations and it cannot be said that accumulation of minute variations really leads to any significant evolution.

4. CONCLUSION

Inasmuch as populations in the large sense are made up of individuals which comprise one or more species, then speciation, i.e., the formation of new species, is the *sine qua non* of evolution at the lower levels at least. For an excellent account of the phenomena affecting speciation the reader is referred to Mayr.¹ Although of necessity much important matter has been omitted, we have given enough information to show how modern genetical evolutionists consider the processes of evolution and speciation occur. Besides the four major factors of mutation, recombination, isolation and selection, which have been described in some detail, there are many others. Indeed, it should be obvious that the whole environment is the laboratory of evolution. Unknown or little known factors tend at present to be grouped under the heading of selection which Wright² described as 'a waste basket category that

¹ 1942. ² 1933, p. 26.

includes all causes of directed change in gene frequency that do not involve mutations or introductions from without.¹ As research proceeds the operational elements in selection are becoming better known, and, in the course of time, this may necessitate modifications in the mathematical models on which modern work is based. But this could only be accomplished by a greatly increased amount of field and laboratory work.¹ Great advances should be made when the evolutionist and the ecologist join forces.

Still, several features stand out at present. The essential condition for the occurrence of evolution seems to be the production among some members of a group of a selective advantage which enables them to increase their numbers in the group. The process is cumulative, but too many and too great changes would probably lead to extinction, and it is at this point that homeostasis seems to be of importance. Constancy is just as important as change in the long run; it is the balance between them that makes evolution the ordered process that it is. A further understanding of the nature of this balance may lead in the future to a better understanding of the mechanistic and teleological aspects of evolution which some people may consider to be of prime importance if we are to find any fundamental meaning in evolution as a whole.

In the interplay of forces leading to change a point is reached when a new species has been formed, and then the basis for advance seems to be an effective isolating mechanism which prevents the new and old species from interbreeding any further and provides opportunity for further substantial change in both species through mutation and recombination.² It seems that geographical isolation will be the most effective in this regard at the beginning because such barriers reduce gene flow from the parental forms back into the new stock, perhaps even down to zero. Nevertheless, a mere increase in the number of species does not necessarily imply evolution except in the restricted sense of

¹ The large electronic computers may prove to be very useful in clarifying the complex pattern of the evolutionary process, and indeed J. L. Crosby (1959) has begun working on the long-term evolution of the common primrose in which many possible factors are incorporated into the calculation done by the computer.

² We may note here that this new species may become present as a single individual, or even, in the case of plants, as a branch of a single plant, or as a number of individuals. The recognition of these possibilities is important concerning the evolution of man.

micro-evolution. It does not imply the formation of new genera, families, etc. Goldschmidt¹ considered that the formation of varieties, races, subspecies, etc., is evolution within the species and is of a different nature to evolution beyond the species. This latter type is what he called macro-evolution for which large mutations are necessary. To Goldschmidt the sub-species is not an incipient species; it is rather a variant adapted to a particular (geographical) environment, and his work on the Gypsy moth (*Lymantria dispar*) supports this idea. In fact Goldschmidt considered that evolution proceeds from the higher categories of organisms down to the species, and not in the more usually considered manner of a procession from the species upwards to the family, etc. Goldschmidt's theory is in line with the geological evidence which shows large gaps between the major groups of organisms.

Many of the orthodox geneticists and neo-Darwinians, however, do not accept Goldschmidt's views. For example, Mayr² considered that all the available evidence indicates just the opposite. He summarized the position by stating that: 'New species arise from isolated and much modified portions of parental species.' And the most convincing proofs for this lie in the three following facts: (a) geographical sub-species are often seen to be of the same kind as the temporal sub-species described by the palaeontologist; (b) isolating mechanisms maintain the distinctions of species. 'To explain species it is necessary to explain the origin of the isolating mechanisms'; (c) nearly all genera of animals contain incipient species or border-line cases. On both of these views, however, selection acts as a guiding factor. The fundamental difference between the views lies in the origin of the change concerned in evolution—in one case the change is large, and in the other it is small, perhaps extremely small. Wright³ pointed out that even for the larger groups, such as families and orders, it is not necessary to postulate equivalently large mutations, because normally a species tends to persist in a state of equilibrium for a very long time. All this time it is accumulating a store of potential variability which if released by a change in the environment may produce very rapid and large changes in the species.⁴ If the larger categories have been produced in this way, then,

¹ 1941. ² 1949b, p. 318. ³ 1949.

⁴ See also Simpson, 1944.

according to Brough,¹ it is possible that selection, except as a negative and purely eliminating agent, is pushed aside during these great evolutionary surges. Brough also considered that the production of the large categories was due to a greatly increased mutation rate compared with the present, rather than to a sudden release of an accumulation of potential variability.

Mention may be made here of the synthetic or experimental species. The production of these species followed from the work on polyploidy mentioned earlier, and the phenomenon is almost confined to the higher plants.² As we learnt earlier polyploids are organisms with chromosome numbers which are multiples of a common basic or haploid number and there are two chief kinds called *autopolyploids* and *allopolyploids*. Autopolyploids are derivatives of straight forms in which the basic chromosome number is doubled, trebled, or quadrupled, etc. On the other hand, if the increase, such as doubling, occurs in a hybrid the resultant organism is called an allopolyploid. The difference between these two types may be illustrated as follows. In a normal pure breeding diploid species the two sets of haploid chromosomes may be represented by *AA*. If doubling occurred in this organism then the resultant would have four sets of similar chromosomes as *AAAA*. This would be an autopolyploid, or in this case autotetraploid (because it has four sets of *A*). The hybrid between an organism with *AA* sets of haploid chromosomes and one with *BB* sets of chromosomes would contain a set of each, i.e., it would be *AB*. If doubling occurred in this then it would contain *AABB*, that is, it would be an allopolyploid or in this case an allotetraploid. In such an organism when meiosis occurred the *A* sets of chromosomes and the *B* sets would conjugate between themselves respectively. Thus meiosis would probably be quite regular and the hybrid would be fertile.

Allopolyploidy has proved to be of great importance in the evolution of plants. There is no doubt that in nature allopolyploids are of common occurrence, and they have been produced experimentally, thus giving direct experimental evidence of evolution at the species and even at the generic levels. The phenomenon was first described by O. Winge in 1917 under the heading of indirect chromosome binding and much work on it has been done by Kihara, particularly on wheat, who showed that the

¹ 1958.

² See p. 180.

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cultivated bread wheats probably arose through allopolyploidy in Afghanistan about 6,000 years ago. We will mention a few examples below. Excellent accounts are given in several textbooks and papers to which the reader is referred for further details.¹ There is no need to describe in detail the cytological mechanism involved in the production of these plants which is well known and has been given in outline above. In 1937 C. D. Darlington gave a list of forty-nine allopolyploids which had been produced in experiment alone up to that time, and since then new artificial techniques have been tried which have produced many others. Almost any investigation of natural plant hybrid populations will give circumstantial evidence of the occurrence and importance of allopolyploids in nature and in evolution.

In 1924 Blackburn and Hattison showed that the wild rose *Rosa Wilsonii* was an allopolyploid derived from a cross between *R. pimpinellifolia* and *R. tomentosa*. In 1929 Skovsted showed that probably *Acca sellowiana* was an allopolyploid derivative of *A. hippocastanum* and *A. paucia*. The horticultural plant *Prunus Kewensis* arose naturally as a branch from a plant obtained by crossing *P. floribunda* with *P. verticillata*.² *Phleum pratense*, a hexaploid, probably arose from a cross between a diploid *P. pratense* and the tetraploid *P. alpinum*.³ Frandsen⁴ showed that *Brassica juncea* may be an allopolyploid produced from a natural cross between *Brassica campestris* and *B. nigra*. Stebbins⁵ gives evidence to show that *Bromus arizonicus* is an allopolyploid derived from a cross between *B. trinitis* and *B. catharticus*. Again, Howard and Manson⁶ gave evidence showing that a wild triploid form of *Nasturtium officinale* was produced from wild diploid and tetraploid forms.

The few examples given above are all of species whose origin has been inferred circumstantially from cytological and genetical data. There are some cases which are more direct and give the confirmatory evidence necessary to support the initial supposition that allopolyploids are of wide occurrence in nature. In 1930 Müntzing⁷ crossed *Galeopsis pubescens* with *G. speciosa* and among the progeny was a triploid which was then backcrossed to the *pubescens* parent. Among the progeny of this backcross was an

¹ See Dobzhansky, 1942, 1951; Darlington, 1937; Waddington, 1939; Stebbins, 1950; Petherill, 1952 and H. A. Allan, 1937 and 1949.

² Newton and Pellew, 1929.

³ Gregor and Samsom, 1930.

⁴ 1943.

⁵ 1947.

⁶ 1946.

⁷ 1930 and 1931.

allotetraploid which Müntzing called *Synthetic Galeopsis tetrahit*. In all respects this experimentally produced plant was indistinguishable from the naturally-occurring wild species called *Galeopsis tetrahit*. It crossed perfectly with the wild species and produces normal offspring. The synthetic species also varies in a manner similar to the wild form. Müntzing claimed that this was the first time a replica of a natural species had been built up experimentally. His work, however, gave no indication of the actual time when the wild species arose in nature. But much more data has been obtained in this regard for the celebrated Rice Grass (*Spartina Townshendii*) which is considered to be derived from *Spartina stricta* and *S. alterniflora*.¹ Although this plant has not been actually synthesized its history is well known. It appeared suddenly in this country towards the end of the 19th century, and at first it was a rare but vigorous plant. At the present time it is widespread along parts of the coast of southern England and is planted to consolidate the mud in which it can grow vigorously. In the wild if it comes into contact with either of its original parents, *S. stricta* or *S. alterniflora*, it dominates and ousts them. *Pentstemon neotericus* is an American plant which is very successful in nature and behaves like the Rice Grass by ousting its parents. J. Clausen² has shown that it probably arose as an allopolyploid from *Pentstemon laetus* and *P. acaeruleus*.

As examples of allopolyploids produced experimentally the following may be mentioned. In each case the allopolyploid is distinct from the parents and generally breeds true. *Nicotiana digitata* was produced by R. Clausen and Goodspeed in 1925 from a cross between *Nicotiana tabacum* and *N. glutinosa*. Doubling of the chromosomes in the F_1 hybrid gave rise to *N. digitata*. *Digitalis mertensiana* is an allopolyploid obtained from crossing *D. purpurea* and *D. ambigua*.³ Several other allopolyploids have been produced in the genus *Nicotiana* by several workers by crossing of several species which is followed by doubling of the chromosome number in the sterile hybrids. One of these, obtained from the cross *N. sylvestris* and *N. tomentosiformis*, resembles *N. tabacum* to some extent. An interesting result was obtained by Nygren⁴ who synthesized *Calanegrestis purpurea* by crossing *C. canescens* and *C.*

¹ See Huskins, 1931, and Dobzhansky, 1942 and 1951.

² 1933 and Clausen, Keck and Hiesey, 1940.

³ Buxton and Newton, 1928.

⁴ 1946.

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epigaea, and also by treating *C. purpurea* with colchicine. A large number of allopolyploids have now been produced mostly by treating sterile hybrids with colchicine or other chemicals. Finally, several fertile allopolyploids have been produced synthetically by crossing different but related genera. Examples of these are *Rapbanobrassica* obtained by crossing *Rapbanus sativa* (radish) with *Brassica oleracea* (cabbage),¹ and *Aegiloptriticum* obtained by Tschermak and Bleier² from a cross between *Triticum durum* and *Aegilops ovata*.

It may be rather premature to say that the experimental synthesis of species is a commonplace, but it is true to say that there are many examples of the production of synthetic types. It is important to notice that most of these synthetic allopolyploids are different from the parents in each case and are true and constant breeding hybrids. In many cases they satisfy the requirements of the systematist for species naming and thus they are regarded as new species. The extension of the artificial production of species to natural categories has resulted in a demonstration of the fact that as far as plants are concerned many of them arose through polyploidy and hybridization, and it is also a demonstration of great value to the evolutionist in providing direct evidence of the evolutionary process in nature. J. B. S. Haldane³ considered that the discovery and description of allopolyploidy has given the most important modification to Darwin's and Wallace's theory of evolution since it was first put forward. To show the importance of this evidence for evolution we may finish this account by quoting J. Heslop Harrison⁴ who wrote:

From the large samples of species that have already been investigated it is estimated that perhaps half of the entire north temperate flora of the world consists of polyploids, and that of these, rather more than half are likely to be allopolyploids. The importance of this process of species formation in the higher plants is thus considerable, particularly when the further fact is appreciated that very many plants which are important in agriculture have almost certainly arisen in this way.

The account of the factors of evolution which we have given has been mostly drawn from the genetical and cytological sides of

¹ Karpechenko, 1927 and 1928. ² 1926. ³ 1959, p. 717.
⁴ 1953, p. 93.

biology. Much evidence regarding the factors of evolution is also available from other branches of biology, such as ecology, for example, and some studies involving these other disciplines have been given in the text as the occasion arose. But we are unable in the limits of this book to go further into these matters. The geological and other types of evidence have been given in earlier chapters. But the modern genetical and cytogenetical picture gives a causal explanation of evolution and at the same time it gives a line of evidence which was not available to Charles Darwin when he first brought together the 'classical lines of evidence' for evolution. The result of all this modern research and study is that we now have before us an increasing body of knowledge, which, if it does not prove that there is an evolutionary process in nature, is rather empty and void of any true meaning. And it is on this basis that the evolutionist takes his stand that evolutionary theory gives a sufficient and reasonable explanation of the progression of living things without appealing to any forces extraneous to empirical science. We may perhaps close this section by giving a quotation from Sewall Wright¹ which summed up the modern experimental conclusion about evolution. Wright wrote:

Perhaps the most important conclusion from statistical genetics is that neither the driving factor nor the actual limiting factor in evolution is ordinarily to be sought in the genetic situation (including the process of mutation) once the stage of the interbreeding species of multicellular organisms has been arrived at. The driving force is the universal tendency of life to expand and to seek out all opportunities. The limiting factor in each case is the ecologic pressure from other species and from the non-living environment, by which the species is ordinarily kept in place.

Evolution is the penultimate expression of life in all its forms on this earth, and finds its antithesis in the entropy of the physical inorganic world. The ultimate expression of life on this earth is to be found in man alone, and the remaining chapters of the book are devoted to this consideration.

¹ 1949, pp. 476-477.

Chapter VII

Evolution and Christians

I. INTRODUCTION

We have now completed our study of evolution (excluding that of man) as seen by the biologist, after first considering the way in which science and biology function, and secondly by realizing that the scientific method, or methods, have their limitations and are not infallible. Equally, we realize that well-founded scientific conclusions are not merely opinions. Scientific conclusions arise from sense data and they are arrived at either by the inductive or the hypothetico-deductive methods of study. Thus the scientist may tend to be impatient sometimes with the philosopher who doubts some scientific finding because of a philosophical difficulty. The scientist may agree that it is the task of philosophy to take over the established conclusions of science and integrate them, but, he may ask, which brand of philosophy must be used for this task? The dilemma thus apparent may be eased when we realize that philosophy also is not infallible; nevertheless, the more universal are the concepts of a philosophy, or philosophical system, the greater chance it should have of integrating scientific knowledge.

Catholics are well aware that the system of philosophy used by the Church, called scholastic philosophy and Thomism, is well adapted for explaining what she wants to explain in as universal, exact and intelligible terms as possible. Inevitably, then, the Catholic may tend to interpret science along traditional philosophical lines, but it may nevertheless happen that some things in science are not suitable for interpretation in Thomistic terms, and other interpretations may be attempted in the light of modern developments in philosophy. If a biological matter seems to stand in opposition to some important philosophical concept the biologist will not discard the matter, but he will wisely suspend final judgment until the issue is clarified. There should not be

dogmatism in either philosophy or science, although there must be 'dogmas' in the sense of truths in both disciplines.

When we come to theology the case is different. Theology is that system of knowledge which considers God and the relation of man to God. Many scientists unfortunately do not believe in God, and even if they do, many will assert that science has no direct relation to God. Theology, it is said, has nothing to do with science, and in a sense this is correct, if by science we mean the day-to-day work of the scientist and nothing more. On the other hand, Catholics believe that God should enter into all our activities and ideas; hence theology, as the study which treats of God, has a part to play. Strictly speaking, theology is the study of God's Revelation which contains absolute truth. Positive science also seeks truth, hence it should be a help to theology and not a hindrance. Positive science and theology should be complementary to each other. A Catholic scientist would assert that any scientific matter which without doubt contradicted Revelation properly interpreted, or the official teaching of the Church, was in error.

As far as evolution is concerned, if it should happen that some matter is really contrary to Faith, the Catholic knows that sooner or later the error of the evolutionary finding will become apparent, and there would be no compulsion on him to accept it. But it becomes the duty of the Catholic biologist to attempt to resolve the difficulty concerned. In this connection it is important to point out that the opinions of individual theologians do not necessarily correspond to the authoritative teachings of the Church. Evolution itself furnishes a good example here. From the time of Charles Darwin and the *Origin of Species* many Catholic theologians opposed the theory of evolution, privately if not openly, for many reasons which seemed legitimate to them and still remain so. The Church said nothing officially about the theory until 1950 when Pope Pius XII mentioned it in a serious statement and he certainly did not condemn it.

Now that we have given a short account of the Catholic attitude to the acceptance of knowledge, we may pass on to the subject matter of this chapter. We hope that this chapter and the next will be the justification of the whole account of evolution which we have given, at least as far as Catholic and other Christian readers are concerned. But it must be remembered that the

opinions presented are purely personal and commit only the writer unless otherwise stated or implied in the text. There are some scientists who may be disturbed because a scientific writer has given an account of a scientific subject and then attempted to connect it to philosophy and theology. They are entitled to their opinion, but so is the writer who contends that if science does not become integrated with all our activities and thoughts, especially that activity which is of most importance to us, then science has merely a utilitarian value.

Faith is a living reality to all men, and it covets all their deepest activities. Even the scientific sceptic who lacks its highest expression in religion, does not escape it, for all that he does depends on faith of some kind. To quote Aldous Huxley:¹

All science is based upon an act of faith—faith in the validity of the mind's logical processes, faith in the ultimate explicability of the world, faith that the laws of thought are laws of things. In practice, I repeat, if not always in theory, such conceptions are fundamental to all scientific activity. For the rest, scientists are opportunists. They will pass from a commonsense view of the world to advanced idealist theories, making use of one or the other according to the field of study in which they are at work. Unfortunately, few scientists in these days of specialization are ever called upon to work in more than one small field of study. Hence there is a tendency on the part of individual specialists to accept as true particular theories which are in fact only temporarily convenient. It is highly unfortunate that so few scientists are ever taught anything about the metaphysical foundations of science.

Thus first in this chapter we wish to draw together the account of scientific evolution which has been given in previous chapters. Next, an account of the evolution of man will be given because this aspect is crucial to any Christian, and then some points of contact of evolution with theological matters will be indicated by way of illustration. Finally we wish to touch on some few points of contact with philosophy and to give our conclusions. In a word, as a Catholic, I wish to see if evolution, and particularly the evolution of man, opposes Revelation and is condemned by the Church.

¹ 1938, p. 258.

2. SCIENTIFIC EVOLUTION

Our short survey of the history of organic evolution showed us that the mere existence of so many kinds of organisms engendered in men's minds an idea of organic evolution. At first, this idea was nebulous and was often expressed in a rather mythological way, but the realization that living things 'sprang from' other living things seems to be a very old idea. With the emergence of science, before and during the Renaissance, the evolution idea was expressed in classifications and gradually more definite and formal concepts emerged until the time of Charles Darwin. Since then various evolutionary theories have been advanced and the subject has been, and is being, vigorously investigated experimentally.

All this is clear to anyone who takes the trouble to study the subject. Still, our readers may easily be left with two large questions unanswered, and these may seem to be the most important of all. They are: (a) what is evolution, and (b) is it proved?

Firstly, what is evolution? The truth of the matter is that different people have different ideas about the subject. We will give some of the most important ones. Firstly, organic evolution may mean that all living things are ultimately descended by way of regular sequences of changes from one or a few primordial ancestors. This idea asserts that at the beginning, when living things first appeared on the earth, there was only one, or perhaps a few, kinds of them, and over the years these have changed to produce the multiplicity of things we know from the records of the rocks and see around us today.

Secondly, organic evolution may mean that all things which are common to a basic type or plan of construction, such as the larger plant and animal classes, or even phyla, are each descended from a common ancestor by changes as the years went by. Here nothing is said about the derivation of these larger groups themselves. Thirdly, we give here a definition by K. Mather¹ as: 'Evolution is the occurrence of persistent changes in the hereditary constitution of a population of organisms.' If any other meanings, or definitions, of organic evolution exist, they will probably be found to be included in one of the above, or an extension of one of them. Some definitions may attempt to connect all of them together.

¹ 1943, p. 1.

One thing in common to all the meanings given above is that evolution is thought of as an evolutionary process in nature. We should point out that an *idea* of evolution arose first, and the recognition of it as a process came later. A philosopher may object and say evolution is not an idea, but the history of the subject shows that there has been, and is, in men's minds a concept of evolution arising from the basic philosophical idea of change. Whenever we mention evolution either as an idea or as a process, it is clear that we imply something which exists also in reality in nature and which we conceive either as an idea or appreciate as a process, according to the context in which the matter is being discussed.

It may be noticed that in the definitions of evolution given the word 'species' was not mentioned. Not so many years ago biologists would have unhesitatingly included this word in a definition of evolution. But in the past the word has involved biologists in so many circular arguments leading to no definite conclusions. A biologist is more aware than anyone that morphological species at least exist in nature, but he hesitates to define the word, unless he gives an empirical definition such as that of Tate Regan¹ which reads: 'A species is a community, or number of related communities, whose distinctive morphological characters are in the opinion of a competent systematist sufficiently definite to entitle it, or them, to a specific name.' The species is thus a peg on which to hang the things we find in nature. This definition is non-committal, and it certainly steers clear of any philosophical connotations which may be attached to the word. A philosopher may be disturbed by a change of *nature* which may be at the basis of *his* conception of species, but the empirical definition avoids difficulties of this kind and accomplishes all that the systematist wishes it to do. Such a definition may be applied quite easily to the definitions of evolution already given. The process of evolution may then be visualized in the nature of changes which occur in communities rather than in individuals, although, of course, changes in individuals are not excluded and are ultimately basic to the whole process.

Now we come to the second question: Is evolution proved? This question is sometimes put in the form 'Is evolution a fact?' Obviously the answer will depend on what we mean by evolution,

¹ 1926, p. 75.

by proof, by fact and the evidence for evolution. Different people again mean different things by these words. To enter into a discussion of their meaning would involve us in lengthy linguistic and philosophical topics which are not necessary here. Absolute fact may be attained regarding objects and their movements around us. The observational facts of science are absolute in this sense in that we either observe them or we do not. The scientist will believe that his fact is true, but he will not call it absolute truth because, as likely as not, he would be doubtful about the meaning of this concept when applied to anything except simple observational happenings or objects. In Chapter 1 we have already discussed the meaning of 'theories'; suffice to say here that the scientist then builds his facts into a theory.

If theories of this kind have a universal appeal and are supported by strong evidence, the scientist regards them as being true, even if it is only approximate truth, until someone demonstrates that they are not so. Some scientists will affirm a theory, such as the evolution theory, in this way, by saying that it describes or explains a true feature of nature so far as the evidence shows. In this sense the biologist may say that evolution is a fact, but he is not then asserting absolute certainty. A theory is true so far as observational facts and logical deduction or induction indicate; a new fact may emerge which may show that the theory is only a partial explanation of the reality in nature. In the light of modern scientific knowledge, however, the scientist knows quite well that theories of universal applicability contain a large measure of absolute truth, and new discoveries will not disprove them completely, although they may cause them to be modified or extended. Evolution is a theory of this type. G. R. de Beer¹ writing of organic evolution and the Darwin-Wallace Centenary, wrote:

With the same confidence as it accepts Copernicus' demonstration of the movement of the Earth round the Sun and Newton's formulation of the laws of this movement, science can now celebrate the centenary of the first general principle to be discovered applicable to the whole realm of living things.

In evolutionary theory very many facts have been discovered relating to comparative anatomy and morphology, geographical distribution, palaeontology, classification, genetics, etc. In each

¹ 1956b, p. 76.

of the lines of evidence the facts remain essentially unrelated, or remain restricted to the narrower field proper to them, but they become beautifully related and can be given a more complete explanation if evolution is postulated. Except in genetics, the evidence for the occurrence of organic evolution is indirect, or circumstantial, because it is dependent on these various independent lines, but it is compelling towards a single general conclusion. Some palaeontologists, however, tend to regard the fossil evidence as more or less direct, and there is much to be said for this view. It would be a serious mistake, however, to isolate these lines of evidence. This was the error of D. Dewar whom we have already mentioned several times. He asserted that evolution stands or falls by the palaeontological evidence alone. Taken by itself comparative morphology, or any of the other sections under which evolution is studied, except genetics, does not *prove* the occurrence of organic evolution. The facts in these sections all find a reasonable explanation in the light of evolution. Each line separately could be said to suggest that evolution has occurred. It is a great mistake when dealing with theories, or occurrences of great complexity, to fall into the fallacy of division.¹ Isolated facts may not appear to be important, but when facts are united or considered as a whole their importance is seen in a clearer and different light. The fallacy of division isolates single aspects of complex matters, removes them from their context, and their meaning is not then so obvious. But biology is not actually made up of separate compartments such as anatomy, etc. The organism is a unity within itself and with its environment. The biologist merely divides the subject into various branches as a working convenience in dealing with complex things. When taken together it is then seen with overwhelming force that all these lines of evidence converge to one conclusion: they all point to a reality in nature, that is, to evolution.

Up to the present no other scientific explanation of the facts on which evolutionary theory is based has been given. The biologist considers that evolution is true. Strictly speaking, he cannot say it is a fact in the absolute sense because of the limitations of his subject, and because of the circumstantial evidence, but he is entitled to affirm that the theory possesses a very high degree of certitude and no scientist really expects to go further than this.

¹ See R. P. Clarke, 1901, p. 442.

In genetics we may say that evolution finds its direct proof in the sense of Mather because persistent hereditary changes *do* occur in populations of organisms. If we bring this to the species level in Tate Regan's sense of the word, we may also say that the method by which some species have arisen has been demonstrated and some have even been synthesized. To a biologist this *is* evolution. It is evolution on the small scale, no doubt, but still it gives a direct example of the changes which the indirect evidence so strongly shows to have occurred. The genetic evidence is direct confirmatory evidence of the evolutionary theory which had been formulated before sufficient was known about genetics to attack the subject experimentally. We are entitled to say that on a varietal, species, or even generic level, evolution is certainly true, but the farther away we get from the species, that is when we come to consider genera, families, orders, etc., we find a progressive diminution in the degree of certitude until we reach the phyla when there is little evidence, either direct or indirect, that these groups have actually evolved from fewer and fewer phyla until we arrive at the original progenitor of all things. The phyla in fact stand apart and distinct in the light of our modern knowledge of them, and they all appear fully formed, or determined, in the rocks. That is the fact. In the nature of things, as we proceed up from the species or community level to genera, families, etc., we note that the numbers available for study diminish very rapidly. And this fact in itself makes it more difficult to obtain the more comprehensive evidence such as we obtain at the species level. There are many hundreds of thousands of species, but only twenty or thirty phyla of organisms, which, of course, are sharply cut off from each other because of their different basic plans. There is no reason, however, why these different phyla should not have evolved from common prototypes, and there is a strong *a priori* possibility that they have done so.¹

Nevertheless, the biologist has always worked on the basic postulate that the organism is a unity in itself, and that nature is a unity in diversity. He expects to find law and order in nature. He does not find any fundamental contradictions in nature, and he expects the laws he uncovers to be generally valid. Hence, if he

¹ Strong arguments, which, however, do not completely overcome the difficulty of the gap between the phyla, have been given by G. G. Simpson (1944, 1953, 1960).

proved beyond doubt that species and even genera evolve, and has shown a great probability also for the evolution of families, he is entitled, on this basis of unity in nature, to consider that the process also underlies the history of orders and classes. The discontinuities between these bigger groups are large, but they are not absolute, and the evidence still points towards an evolutionary explanation. It should be remembered too that there are organisms which are intermediate between the orders and classes, that is, organisms possessing features of more than one order or class, such as *Archaeopteryx*.¹ There is thus no biological reason against the evolution of orders and classes. Further, in his lines of evidence the biologist finds many supporting and hitherto inexplicable facts for the evolutionary conclusion which strengthens it still further. The greatest difficulty for the theory still lies with the phyla. But biological knowledge is only in its infancy and there is good reason to think that stronger evidence of the evolution of the phyla will be forthcoming in the future.

In answer to our two questions, then, we may conclude that it is not definitely proved beyond all possibility of doubt that evolution in the large unrestricted sense of the ultimate production of all organisms from one primary one has occurred. On the other hand, it has been definitely proved that species (and even genera) and communities evolve, that is, that an evolutionary process exists in nature. There is a very high degree of certitude that this process is general throughout organic nature.

The theory of organic evolution is thus a very comprehensive one embracing the whole of the organic world. It unites organisms into one grandiose scheme. It gives a sufficient, intellectually compelling explanation of the multitude of facts which otherwise would represent nature as being chaotic. It enables biologists to see order in nature. It shows the occurrence of law in nature. It shows an unbroken continuity of genetic relationship among all organisms. It shows the most dove-tailed and elaborate system of secondary causes which have so far been uncovered by man. As a progression from simple to complex, or from less perfect to more perfect, it indicates finality in nature and points the way to the end in view.

As regards the mechanism of evolution, or the causes of evolution, following from Charles Darwin's theory of natural selection and Mendel's discovery of particulate inheritance, a

¹ See pp. 139-141 of seq.

modern theory of causal evolution has developed. This theory at present recognizes four major factors in the process. These are mutation, recombination, isolation and selection. It is impossible to separate them one from the other in nature and in evolution, and on the basis of the fallacy of division it is an error to do so. For descriptive and research purposes they may be considered separately, but in nature they act in unison. Hence, it is wrong to say that selection alone is the most important factor in evolution. It is not; it is one of the four factors so far discovered, and in any case it is not as universally applicable as the others, because man himself is to some extent independent of it. Selection itself is a phenomenon which is so obvious, but it is also so complex that it probably includes several other major factors which are not yet appreciated. The future will certainly resolve what we call selection into its components, and it is confidently to be expected that many of the difficulties which various people find in selection will disappear.

In conclusion we may say that organic evolution is nowadays an accepted scientific theory with very few qualified dissidents, and the major features of its causes are understood in some degree. We are not yet able to predict the course of evolution, although in some cases we may control the process. The scientific theory is a basic generalization applicable to all organic nature, and so warrants, even demands, the attention of philosophers and theologians who may extend its interpretation and give us further insight as to its meaning which eludes empirical biology.

3. THE EVOLUTION OF MAN

A. General account

It is a fact that the nature of man is dependent on his physical attributes as well as on his psychical qualities. Although he comprises body and soul, he possesses a unity unique in our knowledge of living things. If life itself is the eternal enigma, spiritual man is the quintessence of that life. In the world of creation he is alone; there is no creature like him. A mere speck in the cosmos, he has the potentiality to rule it. Man is undoubtedly unique. He even simulates the Creator by his activities and productions, all of

which emerge only through the agency of his body. In fact, many people would give pre-eminence to this material side of man, assuming that all his higher qualities are products of it. Man is a body and brain. We do not, however, believe in materialism of this kind, but it is clear that a knowledge of man's body is essential to an understanding of him as a biological and spiritual creature. As knowledge goes, it is only through his body that his connection with the rest of the animate world may be traced. Hence the problem of his origin arises, and it is at this point that evolution enters into the picture. By the evolution of man is generally meant the evolution of physical man,¹ and some evolutionists write as though this were the whole man. But the immaterial part of man is not subject to the laws governing material things, and the evolution of the soul can only be considered in a very special sense meaning development rather than change. Man has not always inhabited the earth; as far as we know geologically, he was not in existence more than a million years ago.

In this section we wish to give a concise account of the evolution of man. It is unfortunately true that many Christians, including Catholics, have been very wary about discussing this topic, or have even denied its possibility outright. The reasons for this attitude are complex, but they are mostly bound up with questions of Faith. It is right that any theory which seeks to prove that man is *merely* a product of evolution and nothing more should be combated and exposed for all its fallacy. A mere denial, however, has never accomplished anything among evolutionists who hold such views. Biology is within its own proper sphere when it seeks to ascertain the evolution of man's body, and in one sense this is one of the highest aims of the biologist. His findings in this regard are subject to investigation and confirmation, but a denial of his objective conclusions would seem to be a negation of the use of our intellects in their proper task of the study of man. In point of fact few, if any, competent biologists or anthropologists, who have made a special study of the matter, doubt that man is the highest expression of the animate creation, and that he has sprung from some lower type of animal. In the light of modern knowledge of physiology, anatomy, palaeontology, etc.,

¹ This important point has been emphasised by W. E. Le Gros Clark (1954) who refers to use the biological term *Homo sapiens* in biology and anthropology.

this conclusion is crystal clear to them. But we should remember that it is a scientific conclusion and is thus subject to all the suppositions on which science is itself based. Science is observation and the question of the nature of man is not entirely subject to sense data, although it may be argued that in a sense all known human activity is basically dependent on experience of some kind. At this point the biologist can join hands with the psychologist, philosopher and theologian. We suggest that a proper understanding of man can only come from a synthesis of all the relevant branches of the knowledge of man.

It is necessary to be clear about two points regarding any discussion of man's evolution which we have already mentioned. First, it is scarcely doubted by biologists and anthropologists that man has evolved from some lower creature. This is not a controversial topic. Secondly, it is not known from what animal or group of animals he has evolved; the line of his evolution is not clear, even today. These two points should always be borne in mind because many laymen reading technical accounts of the matter may easily get confused about the issues contained in the accounts. There is much controversy about human evolution and some writings are emotive in their speculations. It is right, however, that there should be argument and counter-argument regarding a scientific problem which is not solved. But this problem concerns only the 'how' and not the 'fact' of the evolution of man.

This question of the 'how' of the evolution of man will probably remain a controversial issue for some considerable time to come, and it may indeed never be completely solved. Some sixty or seventy years ago some biologists were emphatic that man and apes were more or less closely related, but the present-day view has radically changed. No one now holds that man is descended from any existing ape type. It is futile to look for the missing link between man and gorilla. As long ago as 1918 Chalmers Mitchell¹ wrote: 'Writer after writer, with increasing insistence in recent years, had dwelt on the obvious fact that existing groups (i.e. of Primates) are at most in the relation of collateral descendants of a common ancestor, and the tendency has been to place the common ancestor ever lower and lower on the tree of life.' A word about the expression 'missing link' may

¹ 1918, p. 497.

be salutary. Any creature which possessed some of the characters of man and of anthropoid is in a sense a missing link, but it would not necessarily be *the* missing link, that is, the creature which indubitably connected man with the lower creation showing distinctly the line of man's advance; the point at which ape ceased and man began. It is probable that there are many missing links, but unlikely that there is any one missing link.

Some writers trace man back to a hypothetical generalized type of mammal; while Max Westenhofer¹ considered that man sprang from some type of Selachians and tailed amphibians. Douglas Dewar² stated that Sergi, Berg, Belogolovy, Haacke, Kleinschmidt and others held a similar view. G. Elliot Smith in *The Evolution of Man*³ derived man ultimately from an insectivore. In his pedigree the main stem of mammalian evolution ended in man; the apes, etc., branched off from this stem which passed through a tarsoioid stage and a monkey stage to the beginning of the human family. Sir A. Keith⁴ also derived man from a common main line or stem of monkeys from which also sprang gibbons, gorillas, etc., at different geological periods. H. Klaatsch⁵ and F.G. Crookshank⁶ considered that different kinds of men evolved from the ancestors of different existing ape types. A modern opinion summed up the matter by saying: 'Man's immediate phyletic relationship to the ancestors of the anthropoid group of Primates cannot be doubted.'⁷

Morphologically and anatomically man belongs to the class of vertebrates called *Mammalia*, Order *Primates*. In 1873 St. George Mivart defined the Primates and his definition still stands today. They are 'unguiculate, clavicate, placental mammals, with orbits encircled by bone; three kinds of teeth, at least at one time of life; brain always with a posterior lobe, and calcareous fissure; the innermost digits of at least one pair of extremities opposable; hallux with a flat nail or none; a well-marked caecum; penis pendulous; testes scrotal, always two pectoral mammae'.

Classifications of the Primates vary to some extent, but following the definition of Mivart, S. Zuckerman⁸ gave a classification as detailed below which is generally acceptable. There are three sub-orders with various divisions and families as follows:

¹ 1933, p. 92. ² 1938, p. 93. ³ 1927. ⁴ 1948. ⁵ 1923.
⁶ 1931. ⁷ S. Zuckerman, 1933, p. 169. ⁸ 1933, p. 17.

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Sub-order 1. *Lemuroidea* (Lemurs)

Series: *Lemuriformes* with the families Lemuridae, Indriidae and Daubentonidae (occurs in Madagascar)

Series: *Lorisiformes* with the families Lorisidae and Galagidae (occurs in Africa and Asia)

Sub-order 2. *Tarsioidae* (Tarsioids) with the single family Tarsiidae (occurs in Asia)Sub-order 3. *Pithecoidea* (or *Anthropeoidea*)

Division: *Platyrrhini* (New World Monkeys) with the families Hapalidae and Cebidae

Division: *Catarrhini* (Old World Monkeys) occur in Africa and Asia, with four families

Family 1. *Cercopithecidae*

Sub-family: Cercopithecinae including the Mandrill, Baboon, Gelada, Black Apes of Celebes, Macaque, Mangebey, Patas Monkey, Guenon and Talapoin

Sub-family: Colobidae including the Langur, Snub-nosed Langer, Proboscis Monkey and the Gueteza

Family 2. *Hylobatidae* or Gibbons

Family 3. *Pongidae* including the Gorilla, Chimpanzee and Orang-utan

Family 4. *HOMINIDAE* (Man).

Thus the Primates form a natural zoological group. Some writers have separated Man from this order, but when it comes to definition by the characters of morphology and anatomy this separation is difficult to maintain. We should note that man is classed as a Primate on zoological grounds and not on the basis of other qualities which he may possess. The majority of characters of the body of man can be paralleled among the members of one or other of the remaining families and genera in the order. After an exhaustive analysis of about a thousand characters of lemurs, apes, monkeys and man, A. Keith¹ found that man shared 87

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characters with the gorilla, 98 with the chimpanzee, 56 with the orang, 53 with the Old World Monkeys and 60 with the New World Monkeys. According to this list man shares more characters with the New World, or Platyrhine, Monkeys than with the Old World, or Catarrhine, Monkeys, and the orangs. Yet it is generally assumed that in the Upper Cretaceous Period a primitive group of mammals called the *Menotyphlis* gave rise to a group of prosimians, and from them the Lemuroidea and the Tarsioidae were descended. In the Late Eocene Period the Tarsioids gave rise to both the Catarrhine and the Platyrhine Monkeys. Apes and man are considered to be descended from the Old World Monkeys. The anomaly of more characters in common between man and the New World Monkeys and orangs may indicate, therefore, that man is a relatively unspecialized creature with many primitive features. Man is actually regarded as a generalized form of Primate.

As regards the evolution of man it is obvious that a large part of the evidence will rest on comparison of the bones of living and extinct men and other Primates. In living forms other structural and anatomical features may be compared. But in this regard, it is the criteria of comparison which give rise to controversy in spite of the fact that, according to Zuckerman,¹ human bones should never be confused with ape bones. In all questions of the determination of evolutionary relationships based on comparative anatomy and morphology of living and extinct forms Le Gros Clark² pointed out a source of error due to indiscriminate comparisons of the characters of the animals concerned. For example, man and monkey have the same number of teeth, the same bony components of the skeleton and so on, but it would be wrong to conclude that therefore man is descended from a monkey, or is even closely related to one. Characters of this kind may indeed have been inherited from very remote common ancestors, and thus Clark called them 'characters of common inheritance'. Such characters enable a zoologist to classify organisms properly; for example, man and monkey are both Primates, but they tell us nothing about closer relationships. In contradistinction to these characters of common inheritance, Clark recognized 'characters of independent acquisition' or features which were acquired by, say, the members of a family, after it had branched away from a

¹ 1934. ² 1934.

remote common ancestor. Such characters are peculiar to the members of a family, and they do indicate a true relationship between the organisms possessing them, and, of course, it is these characters which are of importance in questions of the evolution of man from lower organisms.

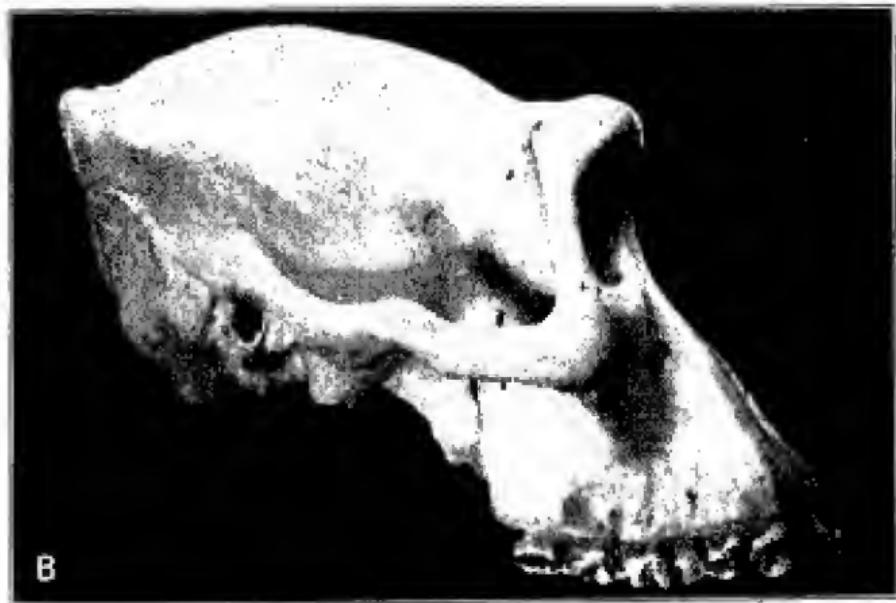
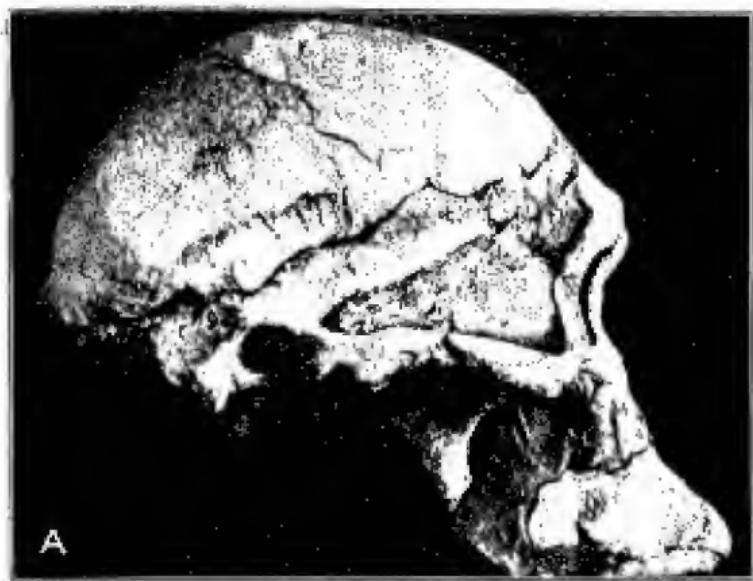
This problem was also ably reviewed by W. L. Straus, Jr.,¹ who gave a list of fifteen of the most important generalized or primitive characters in man and discussed their significance. Because these characters are not commonly seen together in point we give them below from Straus.² They are: 1. The sequence of eruption of the deciduous teeth, involving more particularly the early eruption of the canines. 2. The tendency towards late obliteration of the cranial sutures. 3. The anterior convergence of the mandibular rami. 4. The absence of a backward-projecting simian shelf uniting the two halves of the mandible at the symphyseal region. 5. The comparatively great distance between the thorax and the pelvis. 6. The quadrupedal posture of the hand in which the palm, with extended fingers, is placed against the ground. 7. The comparatively generalized proportions of the hand, particularly relating to the thumb. 8. Essentially generalized features in the hand musculature, especially that of the thumb. 9. The generalized architecture of the ishial region, including the absence of callosities. 10. A relatively long mid-tarsal segment in the foot. 11. Essentially generalized features in the leg and foot musculature. 12. Absence of excessive forelimb development. 13. A primitive sequence of epiphyseal union. 14. A comparatively primitive plan of dermatoglyphics. 15. Absence of a sexual skin in the female.

If we bear these points in mind we can appreciate Zuckerman's³ concise definition of man, which separates him from all other Primates as follows: 'Man is a big-brained Primate with the power of articulate speech. He walks erect and uses his hands—emancipated from the task of carrying his body—to work with artificially-fashioned tools. His teeth, and correspondingly his face, are small relative to those of the apes, and he is omnivorous as opposed to being predominantly frugivorous. These are the essential qualities which distinguish him from the ape, whose capacity for speech is confined to the utterance of sounds the connotation of which is purely emotive, and whose very limited

¹ 1949, and pp. 209-215.

² 1954, p. 323.

³ 1954, 303.



5. A—side view of skull of an Australopithecine and B—side view of skull of a female gorilla. (From Le Gros Clark, 1950b, A after Broom)



6. Skull of *Pithecanthropus erectus* reconstructed by F. Weidenreich from remains in Java. (From Le Gros Clark, 1950b)

ability to use "permanent" tools, as demonstrated in experimental studies, is probably never manifested in the wild.¹ Although this definition mentions articulate speech and the use of tools, it does not directly mention the higher mental faculties. If these were included then man would rank, not only in a different order, but in a different kingdom. There is a wider difference in this respect between 'a man and a gorilla than between a gorilla and a daisy. The one is incapable as the other of creating civilization', as Humphrey Johnson² said. Another definition was given by Le Gros Clark³ but it was designed to limit 'man' to the two species *Homo neanderthalensis* and *Homo sapiens*, thus excluding the older fossil hominids.

Morphologically and anatomically, man, as a member of the zoological family Hominidae, is closest to the family Pongidae which contains the gorilla, chimpanzee and orang. While each of these animals has its own specializations (that is, characters of independent acquisition), which are so advanced as to render it most unlikely that man could be related to them in any other way than as a distant collateral, the kinship becomes more pronounced when functional characteristics are considered. For example, Zuckerman⁴ gave the following functional features shared by man and apes: no breeding season, similar facial movements, diurnal, macular and colour vision, serum precipitin reaction, blood groups A or B or both, related red blood cells, allantoin absent in purine metabolism, menstrual cycle, etc. These may be characters of common inheritance of a not too remote ancestry.

Thus, in a zoological and evolutionary sense, man belongs to the same stock as that of the apes, not by direct descent, but probably by descent from a common ancestor which produced both man and apes. This stock can be traced back also to that of the Old World Monkeys. These animals seem to have sprung from types representatives of which have been found in Lower Oligocene Formations, about forty million years ago.

These earliest types are known chiefly in the form of some fossil teeth and mandibles which are named *Parapithecus*, *Propliopithecus*, *Mesopithecus* and *Apidium*. They were all monkey-like, and *Parapithecus* is perhaps the most primitive member of the

¹ 1943, p. 6. ² 1951, p. 42.
³ 1935, p. 166 and Table 10.

family found to date. Some evolutionists consider that the Hominoidea sprang directly from this, or from a similar type, independently of the apes in the Oligocene Period. By the time of the Miocene Period these earlier forms had advanced to give rise to apes such as *Dryopithecus* and *Pliopithecus*, which were widely distributed and apparently plentiful in Europe, Asia and Africa. All of them were generalized forms, and it is considered that existing types of the family Pongidae and ourselves sprang from them. There is no need to give here any more details about these ancient forms of the Primates, but, if they are indeed the ancestors of the apes and ourselves, it is legitimate to expect that some kind of intermediates existed, and this brings us to those very interesting types called the *Australopithecines*, or Ape-Men, as they are called by some anthropologists, and which have aroused so much interest in recent times. After considering the Australopithecines it will be necessary to examine the fossil hominids and so to those creatures which were undoubtedly men as we know them, that is to say *Homo sapiens*.

First, however, we should mention a type known for many years but which has received an added importance due to recent discoveries. In 1872 P. Gervais¹ described a mandible with teeth found in the Upper Miocene or Lower Pliocene in Tuscany. This was called *Oreopithecus bamboli* and it was considered to be a Catarrhine or Old World Monkey or Cercopithecoid (see classification, page 250), but its exact relationship was a matter of doubt. Other fossil remains of this creature were later found, and then in 1934 Hürzeler² published reconsidered descriptions of about fifty individuals of *Oreopithecus*. Most of these fossil remains comprised jaws and teeth, but limb and trunk bones were also included. Hürzeler concluded that *Oreopithecus* was not a monkey at all, but was hominoid,³ that is, it belonged to the group including man and apes. Furthermore, it differed from the apes, or Pongidae, and was rather hominid, that is belonging to the man and man-like creatures. Then, in 1958, Hürzeler obtained a nearly complete intact skeleton of *Oreopithecus* discovered by coal miners at Baccinello, Italy, about 200 metres below the surface (see also

¹ 1872 and 1876. ² 1934 and 1936.

³ Confusion should not arise between these terms, hominid and hominoid. Hominoid refers to the apes (chimpanzee, gorilla, orang) and man; hominid refers only to man and man-like creatures such as the fossil men; humanoid is a synonym of hominid; while cercopithecoid refers to the various monkeys.

W. L. Straus, Jr.).¹ This material awaits detailed examination, but it should go far towards settling the exact systematic position of *Oreopithecus*, and it may then be found to be a true hominid, or a creature directly ancestral to hominids, a hominoid, a cercopithecoid, or perhaps it may reveal a new branch of Primates. If it is indeed a hominid, or near hominid, it will be of considerable importance not least on account of its age which seems to be at least ten million years.²

B. The *Australopithecines*

In 1925 R. Dart published a report of the Taungs Skull which had been found in a cave at Taungs, Bechuanaland, South Africa. Dart considered it possessed both human and ape features, and he called it *Australopithecus africanus* (the Southern Ape). It was the skull of a young creature. Then, later, in 1936, R. Broom began his searches for other specimens and he found (1938) fossils of three or four adults in a cave at Sterkfontein, near Johannesburg. He called these *Plesianthropus*. In 1938 also Broom described a further skull called *Paranthropus* found in limestone rocks at Kromdraai, near Johannesburg. Since then several other similar and also unrelated fossils have been found in Africa. We give a list of the earliest of these ancient African fossils below. Numbers 1-5 are Australopithecines and numbers 6-10 are other types. Because of their special significance and interest for human evolution, and for descriptive reasons, we will deal with these organisms separately from the hominids, although many authorities consider them to be primitive members of this family.

1. *Australopithecus africanus* (Dart, 1925). This is the Taungs skull, consisting of a nearly whole young skull with some newly erupted teeth. Found at Taungs, Bechuanaland.

¹ 1937 and 1938.

² Since this was written some fresh information about *Oreopithecus* has been published. Dr. Hürzeler has found that this creature possessed features of both man and ape but seemed to be different from either of them. He considers that the group represented by this creature was a separate, distinct, and early branch from the main hominid line of evolution which arose after the Anthropoid line had branched off from the common hominoid stem. As the age of *Oreopithecus* is in the region of ten million years, Hürzeler's conclusion, if correct, indicates that the direct ancestors of man were in existence at least ten million years ago, and that perhaps man is not such a recent arrival on this earth as we have previously been led to believe. Man's evolutionary line may thus stretch far back into the Tertiary Era (see G. Young in a reported interview with Dr. Hürzeler in *The Sunday Times*, June 5 and 12, 1960).

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2. *Australopithecus prometheus* (Dart, 1948). This was found at Makapansgat in the Central Transvaal and consists of the occipital part of a skull, a mandible, maxilla and part of the pelvis.

3. *Plesianthropus transvaalensis* (Broom, 1938). This was found at Sterkfontein, near Krugersdorp and Johannesburg and it consists of a nearly whole adult skull, a mandible and some other pieces of bone.

4. *Paranthropus robustus* (Broom, 1938), which was found at Kromdraai, near Krugersdorp and Johannesburg, consisting of a cranium (or calcaria), the base of a skull, part of a mandible and snout and another mandible.

5. *Paranthropus crassidens* (Broom, 1949a and b), which consists of two mandibles and a metacarpal bone found at Swartkrans, one mile from Sterkfontein, near Johannesburg.

6. *Telanthropus capensis* (Broom and Robinson, 1949), also found at Swartkrans, near Sterkfontein, and it consists of a piece of a jaw.

7. *Proconsul africans* (Hopwood, 1933a and b), from the Miocene of East Africa, consisting of parts of a skull, limb bones and a nearly whole skull.

8, 9 and 10. *Limnopithecus legotet* (Hopwood, 1933a and b), *Limnopithecus evansi* (MacInnes, 1943) and *Xenopithecus kornensis* (Hopwood, 1933a and b) are not very well known and seem to be similar to *Propliopithecus*.

While *Proconsul* has been regarded by MacInnes¹ and Leakey² as on the line of human descent, Hopwood³ was inclined to regard it as nearer to the chimpanzee. This creature along with the two species of *Limnopithecus* and with *Xenopithecus*, although they are recent African fossil finds, are not seriously regarded as being near to man, or intermediate between man and ape. This remark, however, does not apply to the remaining members of this series found in Africa. Many evolutionists regard the Australopithecines as true ape-men. Thus R. Broom⁴ considered

¹ 1943. ² 1946. ³ 1933. ⁴ 1950.

them to be so distinct and important as to constitute a new family of Primates with three sub-families as follows:

Sub-family 1: *Australopithecinae*

species: *Australopithecus africanus*

Sub-family 2: *Parantbrophytinae*

species: *Pseanthopus robustus*

P. crassidens

Sub-family 3: *Archibatrachopinae* (?)

species: (*Australopithecus*) *prometheus*.

The *Telaniotropis* jawbone is different to all of the above and will be considered later.

Difficulties arise over the naming of these fossils. Sometimes they are referred to by a scientific name, sometimes by a popular name, such as the Taungs Skull, and so on. Some writers¹ tend to include them in a single genus, *Australopithecus*, with different species names, and this would probably be the simplest solution to the difficulties arising from their naming, until at least a sufficient number of fossils have been found to warrant a comparative basis for classification.

Since the original discoveries of these fossils in South Africa a considerable number of various kinds of bones and teeth have been found both at Sterkfontein and Kromdraai which are also referable to the Australopithecinae, and there is a large literature about them. Their age is uncertain and indeed Rogers,² who was the Director of the South African Geological Survey, thought that it would never be determined. These fossils are not all of the same age, but they are not separated by any great time interval; and they are generally taken to date from the early part of the Lower Pleistocene Period,³ although Broom⁴ considered that they might belong to the Middle and Upper Pliocene Periods.

The *Australopithecinae* have been described and commented on by many of the foremost workers on Primate evolution.⁵ Morphologically they had characters of both apes and man. Plate 5

¹ See G. Vandebroek, 1914, and Le Gros Clark, 1935.

² 1926, ³ Le Gros Clark, 1955.

4 TQ47

³ Broom, 1923, 1929, 1945, 1947a and b, 1949a and b, 1950; Dart, 1923, 1929, 1948a, b and c, 1949a and b; Gregory and Hellman, 1938, 1939a, b and c; Le Gros Clark, 1940, 1947a and b, 1950b, 1954, 1955; Broom and Robinson, 1948, 1949, 1950, 1952; Broom and Schepers, 1946; Broom, Robinson and Schepers, 1950; Ashton and Zuckerman, 1956; Zuckerman, 1950, 1954; Gregory, 1949, and many others.

shows a side view of the skulls of *Australopithecus* and a gorilla for comparison. Endocranial casts, however, showed that the brain was possibly more complicated than that of a chimpanzee. It has been claimed that the centres of the brain were sufficiently developed to make articulate speech possible. The brain size, as measured by cranial capacity, varied. In *Paranthropus* and *Paranthropus* the capacity was 435 to 650, or even 785 cc.¹ It has been said that the brain sizes were intermediate to those of man and apes, but, according to Ashton,² who made statistical comparisons of chimpanzee and gorilla brains with these fossils, it is doubtful whether the cranial capacity of the *Australopithecinae* was in fact significantly greater than that of the larger apes, but there are strong indications that the brain was relatively larger in proportion to the size of the creature and that it was more highly developed than in the larger apes.³

The jaws were very large and prognathous, but the general pattern was apparently more man-like than ape-like. In general, the teeth⁴ showed over-specialization to an extent which renders it doubtful that they could have been the ancestors of the earliest fossil men, or *Homo sapiens*. The canines and incisors were relatively small, unlike those of the apes, and the canines were flat-wearing as in man; they did not project above the other teeth as they do in apes. There was no diastema (gap) between the canines and incisors and the pre-molars were bicuspid rather than sectorial as they are in apes. In the skull a nuchal crest, which is an occipital ridge of bone stretching across the back of the head, was present, but it was lower down than it is in apes and more like that of the fossil hominids (see later). The eyebrows were heavily built but rather less so than in modern apes; the forehead was rounded in appearance, something like the human forehead. The cranium was higher up in relation to the face than it is in apes. It was claimed also that the foramen magnum, or hole in the base of the skull through which the nerve cord passes, was much further forward than in apes, and nearer in position to that of man. The occipital condyles, or bones articulating the skull to the trunk, were also further forward than they are in the apes. These last two features have been taken as evidence that in *Australo-*

¹ Broom and Schepers, 1946; Broom and Robinson, 1948, 1952; Le Gros Clark, 1955.

² 1950.

³ See Le Gros Clark, 1955, pp. 118-129.

⁴ The teeth were described by J. T. Robinson, 1956.

pithecius the head was balanced on the body as in humans, and that the creature walked erect or nearly so; thus that it was truly bipedal. The hip bone (ilium) resembled that of man very closely in proportionate characters, general pattern and many details, although the bone itself was smaller than that of man. This bone is one of the most interesting and informative features about *Australopithecus*; descriptions have been given by Le Gros Clark in books already mentioned. The ilium bone is thus further evidence that this creature walked erect. Indeed, Broom thought that the hip bone was very like that of a modern Hottentot or Bushman.

The other limb bones of these fossil creatures consist mostly of a femur, tibia, humerus, ulva, some ribs, and some vertebrae. In general they were much more delicate and smaller than the corresponding bones in apes. An excellent and full review of the head and trunk bones of the *Australopithecinae* was given by Le Gros Clark¹ and he concluded that these bones showed none of the specialized modifications characteristic of the Pongidae, or apes, but rather that they resemble the generalized bones of the early fossil hominids.

Opinion varies about these interesting creatures. Some authorities concluded that they were ape-like forms with many human characteristics. Broom and Dart² found some crushed skulls of monkeys with these fossils and they speculated about their social habits, but not many biologists have taken their speculations seriously.³ In 1946 Dart⁴ considered he had found charred bones and the remains of fire hearths in association with an *Australopithecine* fossil from Makapan. But Oakley⁵ and W. L. Straus, Jr.,⁶ were very doubtful about the use of fire by these creatures. Again, Broom and Schepers⁷ considered that they were truly human in spite of ape-like characteristics. Some comparative anatomists, however, have criticized the conclusions of many of the workers on these fossils. In this respect the reader will find excellent critical and objective accounts of these fossils and the statements made about them in papers, etc., by Zuckerman,⁸ Ashton and Zuckerman,⁹ Le Gros Clark¹⁰ and Robinson.¹¹

¹ 1953. ² 1948a and 1949c.

³ See W. L. Straus, Jr., 1957b. ⁴ 1948a.

⁵ 1954. ⁶ 1954. ⁷ 1946. ⁸ 1950, 1954, b and c.

⁹ 1954, 1956a and b. ¹⁰ 1947a, 1950, 1954, 1955.

¹¹ 1962, 1954a and b.

According to Zuckerman and others, it seems that some of the Australopithecine workers have based their conclusions on qualitative estimations of the relative importance of various selected characteristics, and have given opinions whether certain features of the fossils were more or less ape-like or more or less man-like. Zuckerman contended strongly that such opinions, which are not objective, may easily lead to wrong conclusions and also to confusion among readers who do not know the technique of descriptions thoroughly. He considered that likenesses between such fossil bones and those of living creatures can only be settled by quantitative studies, that is, by biometrical and statistical analyses of the points of resemblance and difference. The reason for the need for this approach is because so many of the dental and skeletal characters in apes and men concern differences of proportions and only statistical analysis can give an objective conclusion to any investigation. Thus, Zuckerman and others¹ found, for example, that after such analyses the teeth proportions of *Proconsul* did not differ proportionately from those of a chimpanzee, and the teeth of *Plesiotropus* and *Paranthropus* were not significantly different from those of an orang-utan or gorilla. But some of these conclusions were strongly criticized by Le Gros Clark² and others apparently because of faulty calculations, but the general criticism of Zuckerman still remains valid.

There has also been much argument regarding the nuchal and sagittal crests mentioned earlier. The nuchal crest is a ledge of bone on the occipital or back part of the skull in apes which is not present in man. In apes this ledge provides a starting point for the powerful muscles which hold the ape head in its suspended position. In man the head rests on the vertebral column and such powerful muscles are not necessary. The sagittal crest is a ridge of bone on the top of the skull in the midline running from front to back. Le Gros Clark³ considered that the absence of the nuchal crest in the Australopithecinae indicated that they walked erect, while Zuckerman⁴ considered that, because these creatures had sagittal crests on the top of the skull, they also possessed nuchal crests which perhaps were not prominent, and that probably they did not walk erect.

¹ See Zuckerman, 1950 and 1954, for references.

² 1953.

³ 1954, etc.

⁴ 1956, etc.

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Because of the controversy about the Australopithecines we may fittingly close this section by quoting the conclusions of these two prominent authorities. Zuckerman¹ concluded:

For all that is known about the extent to which the living great apes have diverged from their Miocene forebears, and particularly the extent to which they may have diverged in features of the post-cranial skeleton, it is every bit as likely that some of the Australopithecines represent the forerunners of the modern gorilla and chimpanzee, as that they were the ancestors of some group of protohominids; and far more likely than that, as has been claimed, they were themselves protohominids.

Von Koenigswald observed that in the Australopithecines those with the largest teeth possessed the largest brains, but in humans the largest brains go with the smallest molars. On the other hand, Le Gros Clark² wrote:

In one sense it might appear that the primitive characters of the Australopithecinae—such as the small brain and the large jaws—emphasize the closeness of man to the apes in their evolutionary relationship. But a more careful appraisal of the anatomy of these fossil creatures brings one to a rather different point of view, for it is now clear that, in spite of these primitive characters, they were already at that early time very different from apes in many fundamental hominid characters of the skull, teeth and limbs. And, from what we know of the rates of evolutionary change in general, this makes it certain that the line of hominid evolution must have become a separate and independent line at a much more remote time. In other words, if anything, the South African Fossils emphasize the extent of the *divergence* of the hominid line of evolution from the ape line of evolution.

And he finally concluded that the Australopithecines were members of the family Hominidae belonging to the hominid sequence of evolution, but he was careful to point out that this does not necessarily mean they are ancestral to the other hominid types, *Pithecanthropus* and *Homo*. They could possibly represent an independent branch, but this possibility is not so likely.³

Finally, it is possible that the majority of authorities in this field

¹ 1954, p. 349. ² 1954, p. 390.

³ Clark, 1955, pp. 154-155.

regard *Australopithecus* as really belonging to the family Hominidae, the family to which *Homo sapiens* belongs. Some authorities consider that in some respects *Australopithecus* was in fact more advanced than *Pithecanthropus* (Java man). This form is dealt with later. The question then arises as to whether *Australopithecus* was human. Recently L. S. B. Leakey¹ and his wife discovered a new Australopithecine skull in the Olduvai Gorge in Tanganyika which further strengthens the view that this creature was a hominid. This skull also gives further evidence that the creature was erect in gait, and had a relatively high level of intelligence. The skull, however, is still being examined and final judgment about it cannot yet be given. A most interesting feature about this discovery is that it was found on what is called an occupation floor, that is, a part of the gorge floor which had been occupied probably as a refuge by creatures. In the floor Leakey found some stone tools and evidence of other implements and also broken bones of birds and small animals which had probably been killed and eaten. J. T. Robinson² has also found bone implements from Sterkfontein which is the site of about 100 specimens of *Australopithecus* which he considers show the handmarks of an intelligent mind, most likely that of an Australopith.

C. The hominid fossils

The first human fossil remains found were an Upper Palaeolithic skull from a cave at Schmerling in the Meuse Valley in 1820; and in 1823 the Cro-Magnon Skull, also Upper Palaeolithic, was found by W. Buckland. Both of these, however, are representative of modern man and, since they were discovered, other older types of men, or near-men, have been found. Before describing these fossils it may be advisable to revise the appropriate geological periods and their estimated time scales. The Australopithecines, already dealt with, may of course belong to this family.

The Tertiary Era began about 70 million years ago, and it is divided into the Eocene Period, the Oligocene Period (began about 45 million years ago), the Miocene Period (began about 35 million years ago) and the Pliocene Period (began about 15 million years ago). The Tertiary Era was followed by the

¹ 1939. ² 1939.

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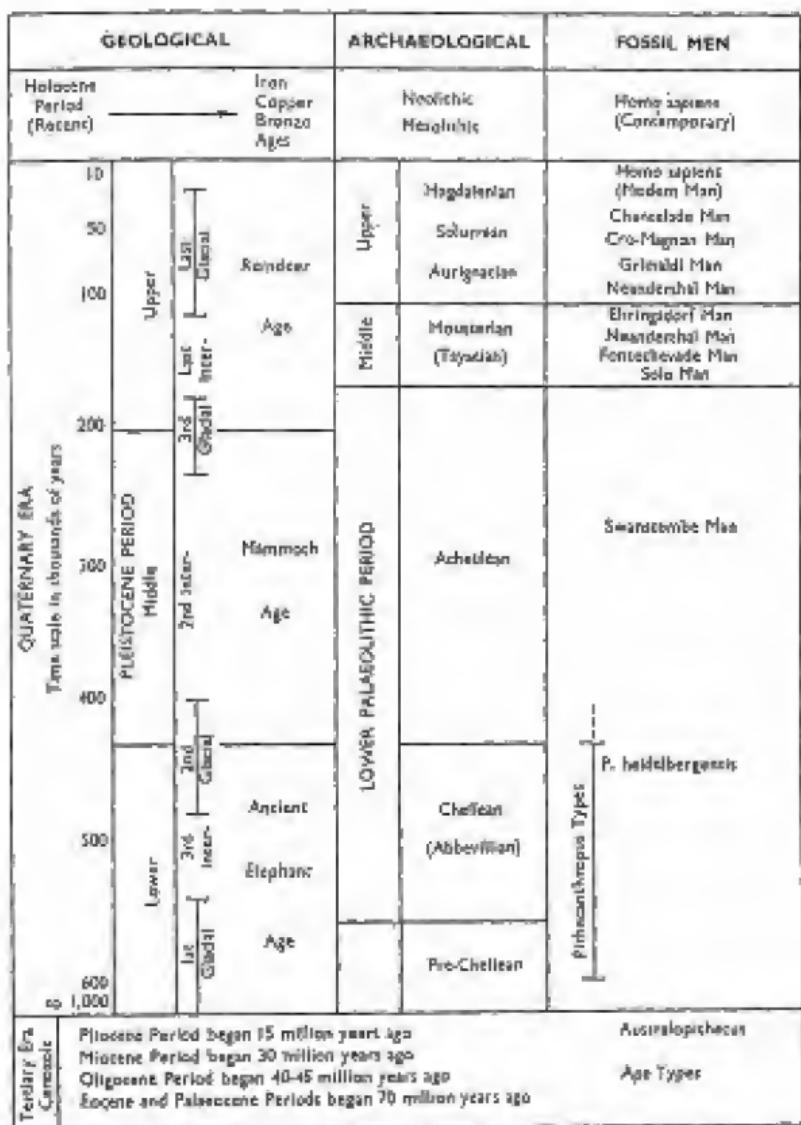


Fig. 22. Chart of the Quaternary Era showing chief geological periods, ages, glaciations and archaeological culture periods with approximate position of the chief fossil men (compiled from various sources).

Quaternary or Present Era which began about one million years ago and which is divided into the Pleistocene and Holocene Periods. The Pleistocene is sub-divided into Lower, Middle and Upper Periods. Culturally, more than half of the Pleistocene is occupied by the Palaeolithic Age which is also sub-divided into Lower, Middle and Upper Sections. These Sections correspond to the following levels of culture attained by prehistoric man: (a) Abbevillian (Chellean) and Acheulean in the Lower Palaeolithic, and this was chiefly the period of the *Pithecanthropus* types; (b) the Mousterian (Tayacian) in the Middle Palaeolithic Period which was the period of Neanderthal and Palestine man; and (c) the Magdalenian, Solutrian and Aurignacian cultural levels in the Upper Palaeolithic. Neanderthal man extended into this level, and it is the period of *Homo sapiens*. These various Periods and Cultures along with the important groups of fossil men are illustrated in Figure 22. The oldest undoubtedly human remains, that is, *Homo sapiens*, called the Swanscombe Skull, dates back about 250,000 years and the Mauer Jaw, which may be human, is much older still.

The fossil hominids (excluding *Australopithecus*) fall into two fairly clear groups in their possession of characters and in time, although there is some overlapping. The archaic group comprises those fossils which are oldest and occur lower in the time scale at the Lower and Middle Palaeolithic Cultural Levels. Thus the Human Family, the Hominidae, is often divided into two sub-families corresponding to these two time groups. The archaic group is called the *Palaeanthropidae*, and the sub-family containing the more modern type is called the *Neanthropidae* (Leakey).¹ For descriptive purposes we will use this grouping.²

The Palaeanthropidae include the following: *Pithecanthropus erectus* (Java man), *P. pekinensis* (*Sinanthropus* or Pekin man), *P. heidelbergensis* (the Mauer Jaw or Heidelberg man), *P. modjoker-*

¹ 1945.

² There is a large and wide-ranging literature on the evolution of man and its aspects. We give a sample of references to various reliable books and papers dealing with the problem either whole or in part as follows: Bergouinoux, 1943; Boigefot, 1946; Boule, 1937; Le Goué Clark, 1940, 1950, 1950b, 1954, 1955; Crookesbank, 1951; Colbert, 1949; Dewar, 1940; Dobzhansky, 1944; Gates, 1948; Houston, 1947; Howells, 1950; Hrdlicka, 1930; Keith, 1930; Klaatsch, 1923; Koenigswald, 1939, 1947; Kroeber, 1933; Krogman, 1950; Mayr, 1950; Piveteau, 1917; Oakley, 1949; Schultz, 1950; Simpson, 1950; Smith, 1927; Stewart, 1950; Straus, 1949; Chardin, 1948; Vallois, 1957; Veldmeijer, 1934; Washburn, 1950; Weidenreich, 1941, 1956a; Zuckerman, 1933, 1934; and Zeuner, 1946.

manus (juvenile *P. robustus*?), *P. soloensis* (Solo man), *Meganthropus palaeojavanicus*, *Gigantopithecus Blackii*, *Telanthropus capensis*, *Homo neanderthalensis* (Neanderthal man, including what McCown and Keith¹ called *Palaeanthropus ehringsdorffensis*, *P. neanderthalensis*, *P. krapinaensis* and *P. palistinensis*), *Homo rhodesiensis* (Broken Hill or Rhodesian man), and *Homo steinheimensis* (Steinheim man).

The Neanthropidae include the following: Swanscombe man, Fontéchevade man, *Homo sapiens* (including Upper Palaeolithic and Modern man).

It is now necessary to give a short account of these fossil men. Many details will be omitted, but sufficient information will be given to enable the reader to form an opinion as to the relative position and type of these creatures, at least regarding the earliest specimens. For very full descriptive accounts in one volume, the reader is referred to the classic work by Marcellin Boule—the fifth edition is by H. Vallois² and is available in English translation by Michael Bullock; also to volume 7 of *Treatise de Palaeontologie* by J. Piveteau³ called *Primates: Palaeontologie Humaine*, in French; and also a shorter but excellent book by Le Gros Clark called *The Fossil Evidence for Human Evolution* (1951).

a. The Palaeoanthropidae

For descriptive purposes these hominids fall into two fairly well-defined groups both as regards their appearance and the period during which they lived. These groups are: (a) the earlier Palaeoanthropidae, which, for the most part, lived in the Late Lower and Middle Pleistocene Periods characterized by the *Pithecanthropus* type of hominid, and (b) the later Palaeoanthropidae which, for the most part, lived in the Late Middle and Early Upper Pleistocene Periods characterized by the neanderthaloid types.

(i) *The earlier Palaeoanthropidae.* In 1890 Dubois⁴ discovered a small piece of mandible (now often called Mandible A) in the banks of the River Solo in Central Java. Then in 1891-92, at Trinil on the same river, he found a skull, a thigh bone (femur) and three teeth. Two of the teeth seem to be those of an orang and the third is doubtful. The skull cap was like that of a human, but was generally flattened in appearance, small and had large eyebrow prominences. An endocast of this skull cap showed that the

¹ 1939. ² 1957. ³ 1957.

⁴ Dubois published his monograph about these fossils in 1894.

brain it once contained had convolutions which seemed to be intermediate in complexity between those of man and ape. The femur seemed to be human and its shape indicated that the creature which possessed it must have walked erect. Dubois considered that the skull cap and femur at least belonged to the same individual, and he thought that this individual was a primitive man intermediate between man and ape and so he called it *Pithecanthropus erectus*. This skull cap and femur are now referred to as *Pithecanthropus* 1.

A large number of other plant and animal fossils were also found at Trinil, but intensive search failed to reveal any further human or near-human ones until 1936-39 when G. H. R. von Koenigswald discovered a series of important remains at Sangiran, also on the River Solo, and in the Trinil beds. These were, in 1937, Mandible B, consisting of a large piece of a jaw with some teeth in their sockets, and also alveoli. In 1938 he found (a) *Pithecanthropus* 2 (or Skull 2) consisting of a much more complete piece of skull than *Pithecanthropus* 1 found by Dubois, and (b) *Pithecanthropus* 3 (or Skull 3), which consisted of a piece of the roof of another skull of a young individual. Then, in 1939 he found *Pithecanthropus* 4 (or Skull 4) consisting of a considerable part of the back and side portions of a skull with an upper mandible containing many of the teeth. This was found at Modjokerto and is called *Pithecanthropus modjokerensis*. Von Koenigswald in 1937 also found pieces of two other mandibles at Sangiran. The first one of these may have belonged to an ape, but the second one was of giant size and thickness and he called it *Meganthropus palawanicus*.

Morphologically these Javanese fossils fall into a more or less common type, at least as regards *Pithecanthropus* 1, 2 and 3 (see Plate 6 for a reconstruction of *Pithecanthropus*). We have already mentioned the human-like femur and the prominent eyebrows which of course reduced the size of the forehead; in fact the forehead began to slope backwards immediately above the massive eye ridges. The jaws projected, that is, they were prognathous, much more so than in modern man, but much less so than in the ape, and the chin receded sharply. The teeth were human with individual variations. The canine tooth was relatively large and projected slightly above the other teeth in some specimens. The cranial capacity probably varied from about 800 cc. to 1000 cc.

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On the other hand, *Pithecanthropus* 4 is rather different. According to Weidenreich,¹ however, it is more primitive than the other forms and he called it *Pithecanthropus robustus*. The skull was larger than the others, and there was a diastema (gap) between the teeth. The second upper molar was large in comparison with the other molars, and the palate itself was different. The form of the dental arch (that is, the outline made by the jaw) was intermediate between the U-like arch of the ape and the parabolic type of modern man. Thus Weidenreich divided these fossils into three groups as follows: (a) *Meganthropus palaeojavanicus*, (b) *Pithecanthropus robustus* and (c) *P. erectus*. Von Koenigswald, however, considered that *Pithecanthropus* 4 should be referred to as *P. modjokertensis* and was probably an adult form of the immature skull also called by this name and found by von Koenigswald at Modjokerto in 1936. Zuckerman² was very doubtful whether *Meganthropus* should be considered a true giant hominid warranting the creation of a new genus. He pointed out that it may just have been a specimen whose large size was perhaps due to some unknown pathological process. Besides, only a piece of a mandible of this creature has so far been found. Le Gros Clark³ considered that all these fossils belong to one genus, so far as we know at present, and that there may have been subspecies among them.

It is possible that these fossils may differ in age. Their absolute age is difficult to ascertain, but they all belong to the Trinil beds which are usually said to be Late Lower or Early Middle Pleistocene, of about half a million years ago. The associated fauna, however, falls into two groups. First, that called the Trinil fauna in which *Pithecanthropus* 1, 2 and 3 were found, and secondly, that called the Djetis fauna in which *Pithecanthropus* 4 and *P. modjokertensis* were found. From comparison with similar beds found elsewhere, it has been suggested that the fossils associated with the Djetis fauna are rather older than the others.

In the Javanese fossil beds there is no evidence that *Pithecanthropus* used fire, or made primitive tools of any description. It can never be certain also whether the skull fragments belonged to similar types as those possessing the other bones which were found, because of the fact that the Trinil beds have probably been disturbed by natural agencies. At one time there was a great deal of controversy about the 'ape-man' of Java, but the position of

¹ 1945.

² 1930, p. 444.

³ 1935, p. 87.

both Java man and of Pekin man was settled among the hominids by the discovery of the latter.

In 1927 D. Black¹ discovered a single molar tooth in a cave at Choukoutien, south-west of Peking. Anatomically the tooth was human but was sufficiently different from those of modern man to enable Black to take a bold step and erect a new genus of man called *Sinanthropus*, or Pekin man. Later, in 1928, pieces of skull were found, and then in the following year a nearly complete skull with pieces of jaw and teeth were unearthed. Since then, numerous human fossil remains have been found and there are now about six nearly complete skulls, eight pieces of skulls giving the remains of about fourteen individuals of various ages, and also eleven pieces of mandibles with eighty-three teeth in place and sixty-four loose teeth which probably belonged to about thirty or more individuals, and also five thigh bones, an atlas, a collar bone, a wrist bone and another arm bone. When Black died the work of describing these fossils was taken over by Weidenreich who died in 1948. During the Japanese invasion of China these valuable fossils disappeared and have never been heard of since, but their detailed descriptions are of course still available.

An important point about all of these remains is that it is certain they all came from a common type of creature, unlike the Java fossils where the bones of many other fossil animals were found. In Choukoutien the only other associated Primate fossil was the remains of a monkey.² Teilhard de Chardin³ and W. C. Pei⁴ regarded the age of these fossils as dating from the Lower Pleistocene and this is the generally accepted view, although de Terra thought they may be Middle Pleistocene.

Morphologically the bones of the Chinese fossils resemble those of the Javanese ones very closely (see Plate 7). The bones, other than those of the skull, are practically identical to those of modern man, and thus Pekin man was erect and bipedal. In general the skull bones and teeth were nearer to those of modern man than to those of *Pithecanthropus* and the brain may have been rather larger varying from about 850 to 1300 cc. (average about 950 cc.). The average of *Pithecanthropus* and *Sinanthropus* together is about 900 cc., which is considerably lower than the average of about 1500 cc. for modern man.⁵ Detailed examination both

¹ 1933.

² Black, 1933. ³ 1937.
+ McDonell, 1904.

⁴ 1939.



7. Lower jaw of *Pteromyscus sharasi* (Gaudichaud):
1—male and 2—female. (From Vallois, 1917 after
Weidenseich)



A



B



C

B. Reconstructed skulls of (left) gorilla, (centre) *Pithecanthropus sinensis*, (right) modern Chinese; A—full face, B—left side, C—back view. (From Valluis, 1957, after Weidenreich)

morphologically and biometrically has shown that among the Peking remains themselves there is a good deal of variability, and also that Pekin man and Java man do not differ significantly from each other. They have fifty-seven characters in common and only four characters which differ. Both Weidenreich¹ and von Koenigswald² were agreed that they belong to the same type of man. Thus Pekin man is included in the same genus as Java man and is called *Pithecanthropus sinensis*.

In the caves at Choukoutien roughly fashioned quartz implements of a very primitive type were found indicating that Pekin man hunted. In fact, a large number of bones of other non-Primate animals were also found which suggests that Pekin man killed and brought these animals into his caves. Pekin man may also have been a cannibal because some of the human skulls suggest that they had been deliberately injured. Remains of hearths were also found so that *P. sinensis* was probably acquainted with the use of fire. All these features show that Pekin man was a true man, but of a low cultural level compared with the earliest modern men as beffited a creature with a relatively small brain, although there is no absolute correlation between size of brain and intelligence.³ Black found that there was a slight difference in the size of the right and left cerebral hemispheres which he interpreted as showing that Pekin man was right-handed and could use articulate speech. In spite of the paucity of evidence showing the cultural level attained by Java man, the fact that Pekin and Java men are morphologically the same means that the Javanese hominid was also a true man. Thus the genus *Pithecanthropus* represented a very primitive type of human being definitely in advance of any ape, but showing certain ape-like features (Plate 8 shows a comparison between the skulls of a gorilla, *Sinanthropus* and a modern Chinese).

In 1935 von Koenigswald bought three molar teeth in a chemist's shop in Hong-Kong which were very large indeed. They were either the teeth of an ape or of a man, but as the crown of one of them was about 22 mm. long (compared with the ordinary human length of 10.7 and 17.8 for the gorilla), von Koenigswald put them in a new (ape) genus called *Gigantopithecus Blackii*. Weidenreich, on the other hand, thought these teeth were those of a true man-like giant.⁴ Others have regarded them as a

¹ 1939.

² 1939.

³ See Vallois, 1937.

⁴ 1941.

type of Asiatic Australopithecine. Recently J. Hillaby¹ reported the discovery of a fossil lower mandible which has been referred to *Gigantopithecus Blackii*. It was found in a cave in South China. W. C. Pei regarded it as probably the jaw of a giant ape. A description of this jaw was given by W. L. Straus, Jr.,² and it seems, from the meagre information available, that it may be the jaw of an ape rather than that of a giant hominid or Australopithecine.

The *Telanthropus* jawbone, discovered in South Africa by Broom and Robinson in 1949,³ was found in limestone of a different colour to the surrounding material. The jawbone is nearly complete and has five molars; a piece of another lower jaw with two molars was also found. The molar teeth were of human type but primitive, and they enlarged in size from the first to the last. The jaw symphysis was thick and the chin receded, but less so than in *Meganthropus*. This fossil does not seem to be an Australopithecine. Broom and Robinson distinguished *Telanthropus* from *Paranthropus crassidens*, the Australopithecine which was found in the same cave as *Telanthropus*, by the characters of the mylohyoid groove which they thought was similar to that in man.⁴ But W. L. Straus, Jr.,⁵ however, showed that this is not a reliable character on which to determine a new genus or relationship. Perhaps it rather resembled *Meganthropus* and the Heidelberg (Mauer) jaws, although the *Telanthropus* jaw is smaller than either of these two. On the other hand, it was possibly nearer to the *Pithecanthropus* type than to the *Australopithecus* type or Heidelberg man. The date of these fossils is not definite, but they are at least as old as some of the later Australopithecines, hence primitive man may have been in existence along with the latter.

In 1931 Oppenoorth found eleven crania (skull caps) and two tibia or shin bones at Ngandong on the River Solo in Central Java, only a few miles from Trinil. Unfortunately the face region and jaws were missing in all specimens and the base of the skulls had been damaged (see Plate 9). The brows, however, were heavy and ridged, the foramen magnum appears to have been in the human position, and the brain capacity averaged about 1200 cc. The tibia was characteristically like that of a modern man. This type of fossil was called *Homo soloensis* (Solo man) at first,

¹ 1953a. ² 1957. ³ 1949 and 1950.

* The mylohyoid groove in the lower jaw runs downwards and forwards from the mandibular foramen through which in life the mylohyoid nerve and vessels pass.

⁴ 1956.

because it was thought to resemble Neanderthal man to some extent. However, Weidenreich and others later considered it was probably closer to *Pitbecanthropus* and thus it has also been named *P. soloensis*. The age of Solo man is Middle Pleistocene, corresponding to the Mousterian Cultural Level, although no implements were found near it and there is no evidence that the creature used fire. *P. soloensis* was thus alive at the same time as the neanderthaloids, and in the evolutionary sense it is considerably younger than the remaining members of the genus *Pitbecanthropus* which only extended into the Lower Middle Pleistocene Period, a difference of perhaps some 200,000 years.¹

In the Lower Pleistocene of Europe a massive mandible was found by Schoetensack in 1908 in a sand pit at Mauer, near Heidelberg. Hence it is often called the Mauer or Heidelberg Jaw (see Plate 10 and Figure 23). In general appearance it looks like a lower jaw of the *Pitbecanthropi*, and it is considerably larger than the jaw of modern man. The vertical ramus, or posterior ascending part of the jaw, is very large and ape-like, and the sigmoid notch is shallow. But the teeth are typically human, although larger than normal teeth, but they are much nearer the modern type than those of Pekin man. There was no chin. This mandible has been referred to the genus *Pitbecanthropus* and called *P. heidelbergensis* on account of its general superficial appearance, but the teeth do not support this view. No evidence of its cultural level has so far been found. There is some evidence that Heidelberg man is the oldest type of human fossil above *Pitbecanthropus*, that is, of a very old Chellean age, practically contemporaneous with Pekin man. If this is so, then Heidelberg man is much older than the Swanscombe man. Vallois² considered it is strictly intermediate between apes and man, and thought that it may show a close relationship to *Homo neanderthalensis*.

A recent discovery in the Ternifine deposits in Algeria was made in 1954 by C. Arambourg and M. Hoffstetter³ consisting of two lower jaws. A year later they found another lower jaw and a parietal bone. These structures were the bones of a hominid, and although they have not been fully described, they show very primitive features (see Plate 11). There was no chin, the ascending rami were strong and large, and the teeth were large

¹ See also Vallois, 1957.

² 1957, p. 177. ³ 1954, 1955a and b.

with low crowns. The parietal bone was very large and the cranial vault was probably low. The date of these fossils is Early Pleistocene, possibly the second interglacial period, or even earlier, some 300,000–400,000 years ago.

These new fossils have been called *Atlanthropus mauritanicus*. It seems that they are definitely of human type, but differ from modern man and from Neanderthal man. Arambourg con-

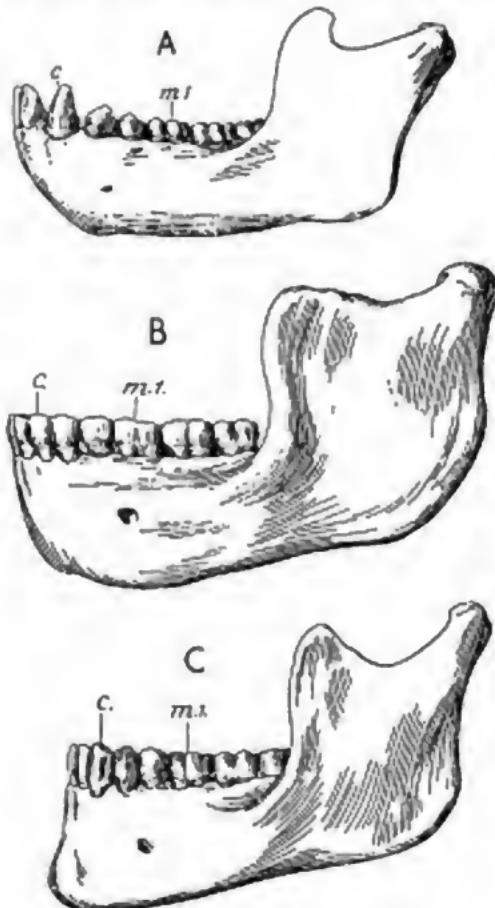


Fig. 23. B—the Heidelberg jaw compared with A—that of a chimpanzee and C—that of a modern man; c = canine tooth, m.1 = first molar tooth. (From Le Gros Clark, 1936b.)

sidered that they resemble the *Pithecanthropus* type most closely, but are rather in advance of them. If this is true, then *Atlanthropus* helps to connect that other giant jaw called *Meganthropus* also with the pithecanthropines, as W. L. Straus, Jr.¹ indeed suggested. *Atlanthropus* is a very important find because it shows that very primitive men may have been in existence in Africa in very early times, and although it may not be identical to *Pithecanthropus*, it is still a very primitive form. Thus the remains of ancient men have now been found in Java, China and Africa which means that man, or man-like types, were possibly world wide in distribution before half-way through the Pleistocene Period.

(ii) *The later Palaeoanthropidae.* In 1848 in a Gibraltar cave a piece of a rather small skull was found, but its significance was not realized until some years later. Then, in 1859, Fuhrrott obtained a cranium which had been found by workmen in a cave in the Neanderthal Valley near Dusseldorf along with some ribs and limb bones. Fuhrrott realized that these were the remains of a primitive type of human being, but this fact was not accepted until later. The specimen was called *Homo neanderthalensis*. In this skull the eyebrow ridges were highly developed, but less so than in earlier forms of man. The forehead was receding and the top of the cranium was flat. Next, beginning in 1866, a series of fossil remains was unearthed. In 1886 a large toothless mandible was found near Dinant, and two good skulls, one with a mandible, were found at Spy, near Namur. With these later bones fossils of the woolly rhinoceros and the mammoth, and more important, implements of the Mousterian Level, were also found in close association. The mandible attached to one of these skulls was large, but it was not the same as the Mauer jaw, and there was no chin eminence. Comparison of these fossils showed that they all belonged to the same type or species.

Later remains have also been found, among them the La Chapelle-aux-Saint specimen in 1908,² the La Quina specimen in 1911, the Le Moustier Skull in 1909, a large number of specimens at Krapina in Croatia, and also in Ehringsdorf near Weiner. Others were unearthed at St. Brelade's Bay, Jersey, at Mount Carmel and Galilee in Palestine, in Saccopastore and Monte Circe in Italy and also in Russia and Africa. Up to the present these remains are all of similar type and represent about 58 or 60

¹ 1936. ² See M. Boule, 1911-1913.

individuals of both sexes and of different ages found in many parts of Europe, Asia and North Africa uncovered by the ice of the last glacial period.

There is a good deal of variation among these skeletons, but biometric studies by G. M. Morant¹ have shown that they are not more variable than a sample drawn from a single population. As there are so many of them it is possible to give a sound description of the type. The skeleton as a whole was heavily built. The skull was moderately large with relatively thick walls. The capacity of the brain averaged about 1450 cc., which is near the average of about 1500 cc. for modern man. The forehead receded quickly. The eyebrow ridges were large, thick and prominent; the rear, or occipital, region of the skull projected backwards, and the vault of the cranium was much flatter than in modern man. In the specimens of men, women and children discovered in Palestine (*Homo palistinensis*), which are neanderthaloid, variations are shown which approach the modern type in that the occipital region of the skull projected less, and hence was more rounded, the apex of the cranium was not so flat and the forehead receded less than in the more typical neanderthaloid. The forehead also receded in the Ehringsdorf specimen. In Neanderthal man the jaws were massive, prominent, and thus relatively prognathous. The chin receded without any prominence, but the specimens found at La Quina and La Ferrassie had the beginnings of a true chin and the face was not prognathous. The foramen magnum was inclined at a different angle to that in modern man, but still in a position sufficient to allow for an upright gait. The ascending ramus of the jaw was broad and large. The teeth were human but large and showed a very characteristic variation in that the molar roots were fused. The skull and face of the neanderthaloids must then have had a distinctly ape-like appearance, but not so pronounced as that of the earlier *Pithecanthropi*. Plate 12 shows the La Chapelle-aux-Saint skulls compared with modern human and chimpanzee skulls.

The post-cranial skeleton was humanoid with many variations compared with the skeleton of modern man. It is not necessary to describe these in detail. In general the bones were massive and thickset, giving the creature a heavy animal-like appearance. The femur was distinctly slightly curved, which, in conjunction with

the angle of the foramen magnum, may have given Neanderthal man a pronounced stoop (see Figure 24). The drawing in Figure 12 was originally made by M. Boule,¹ the great authority on the neanderthaloid type specimen from La Chapelle-aux-Saint. For

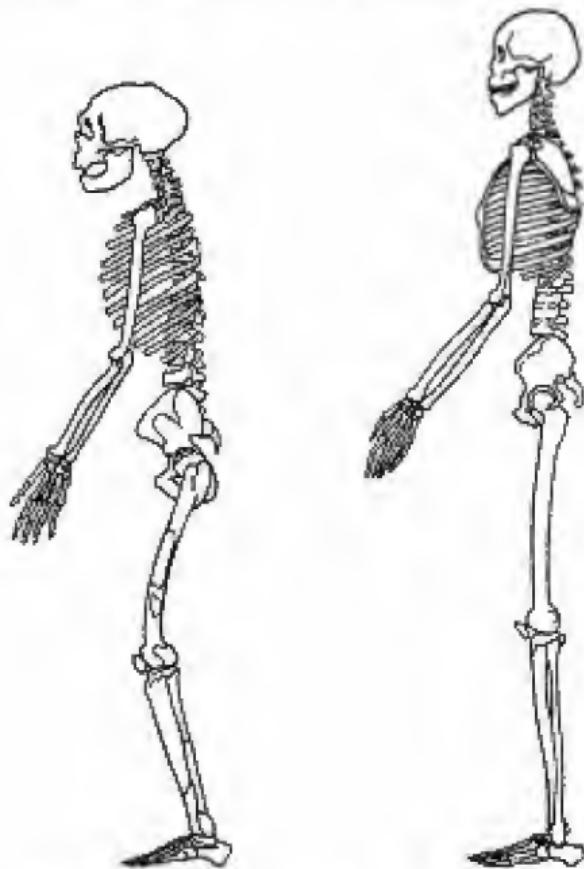


Fig. 24. Left, skeleton of fossil man from La Chapelle-aux-Saints; right, skeleton of an Australian. (After Vallois, 1957.)

many years it was accepted that Neanderthal man did not walk quite erect. But, in recent years, this has been seriously doubted. A critical account of the state of the original fossil bones of this man was given by W. L. Straus, Jr., and A. J. E. Cave,² who, along

¹ 1923. ² 1957.

with C. Arambourg¹ and E. Patte,² came to the definite conclusion that Neanderthal man walked as erect as modern man. It is interesting to note that the *Chapelle-aux-Saint* skeleton was very badly distorted by what was possibly some form of osteoarthritis which would have rendered Boule's task of description very difficult.

The nomenclature of these forms of man is not settled, but we have given the types recognized by McCown and Keith.³ These authorities used the name *Palaeoanthropus* as a generic name to the whole group of neanderthaloids, and they recognized the following species—*Palaeoanthropus neanderthalensis*, *P. krapina*, *P. palistinensis*, and *P. ehringsdorffensis*.

In 1921 some further remains were found at Broken Hill in Rhodesia. These remains were called Rhodesian man or *Homo rhodesiensis*. They consisted of a practically complete skull with jaws and teeth, a piece of an upper mandible, a sacrum, a hip bone and pieces of limb bones. The skull bones are generally regarded as human and neanderthaloid in the jaw which was rather prognathous, with very prominent eyebrow ridges projecting above but not at the sides. On the other hand, the cranium apex was relatively high and less flat than in the neanderthaloid skulls and thus appears to have been more modern. The brain capacity was about 1300 cc. which is relatively large but distinctly smaller than the average for *Homo sapiens* or Neanderthal man. The other bones are similar to normal bones of modern man (see Plate 13).

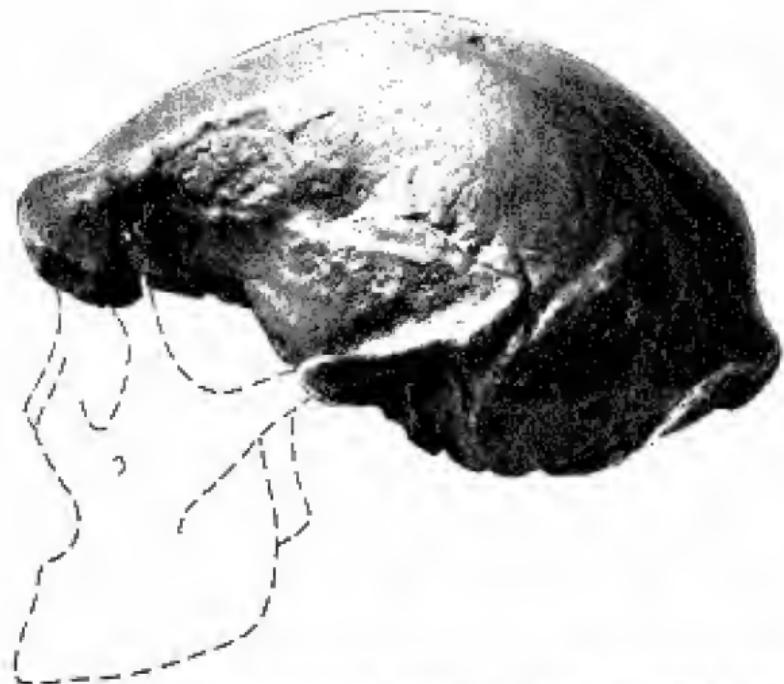
Associated with the bones of Rhodesian man various bone and stone tools were found. The age of these remains is uncertain. Some of the teeth were decayed which suggests that the fossils may only date from the Late Pleistocene; on the other hand, the primitiveness of the associated tools (Cultural Level Oisian) suggests the Middle Pleistocene as their Period. Rhodesian man resembles *P. soloensis* to some degree.

In 1933 an interesting skull called the Steinheim Skull (*Homo steinheimensis*) was discovered at Steinheim which dates from the Late Middle Pleistocene (Riss glacial period), about 200,000 years ago, although its age is not known with certainty. It is probably older than all the neanderthaloid types, but is approached in this respect by the Ehringsdorf skull and the Krapina fossils. This Steinheim skull still shows some neanderthaloid features such as

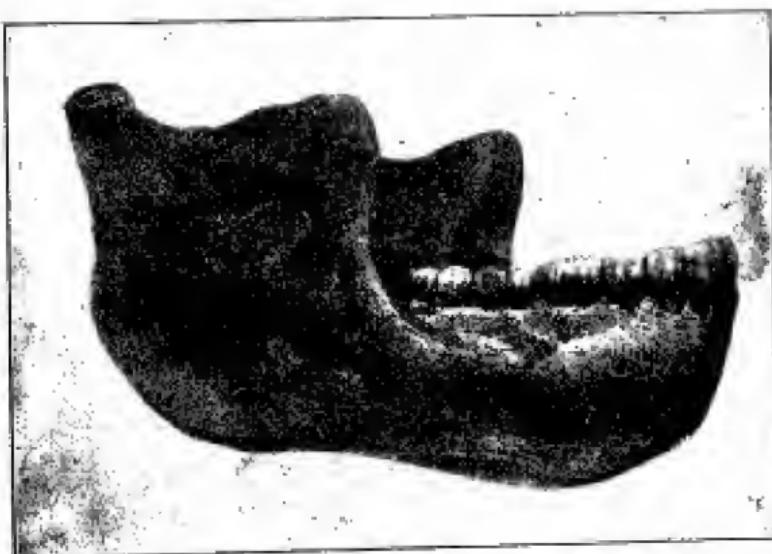
¹ 1915.

² 1931.

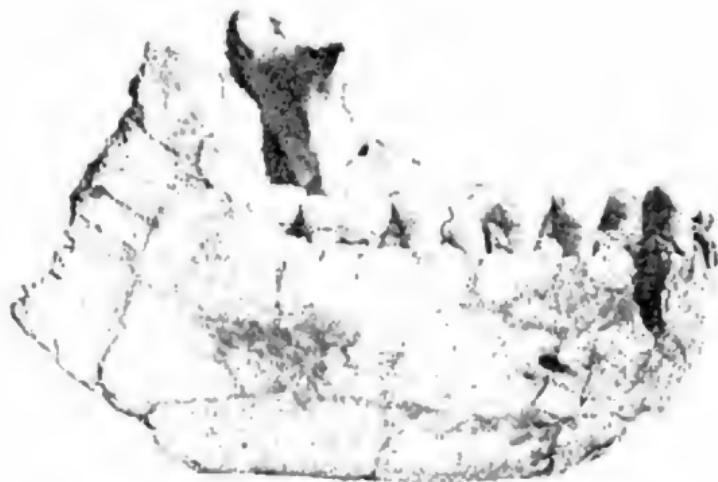
³ 1939.



9. *Homo soloensis* (*Pithecanthropus soloensis*), a skull cap from Ngandong, in Java. (From Le Gros Clark, 1950b)



10. The Heidelberg (Mauer) jaw. (From Vallois, 1957 after Schuerensack)



11. Jawbone of *Australopithecus mauritanicus*, profile view. (From Vallon, 1957)



12. Comparative side views of skulls of (left) La Chapelle-aux-Saints, (centre) chimpanzee and (right) modern Frenchman. (After Vallon, 1957)



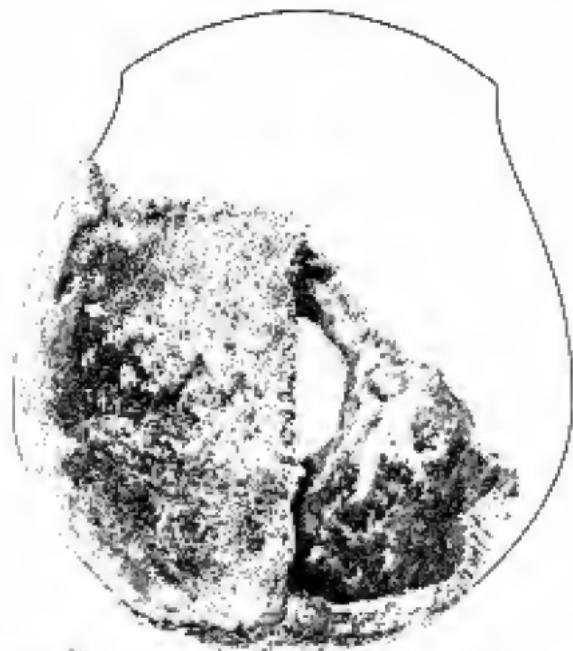
13. The Rhodesian skull,
A—face and B—side view.
(From Le Gros Clark, 1950b)



14. The Steinheim skull. (From Veltius, 1957)



A



B

15. The Swanscombe skull. A—left parietal bone from behind placed beside a right parietal bone of a modern European. Note the similarities and greater thickness of the Swanscombe bone. B—the occipital and left parietal bones superimposed on a top view of a skull of a modern man. (From Le Gros Clark, 1950b)

the rather prominent eyebrow ridges and a heavy upper jaw (see Plate 14). On the other hand, the skull as a whole has a distinct human appearance which is due to the high vault of the cranium and the curved non-protruding occipital region. The capacity of the cranium, however, is fairly small, being only about 1100 cc. Le Gros Clark,¹ however, considered the Steinheim skull to show a combination of morphological characters which does not warrant its separation from *Homo sapiens*. If this is correct then this creature is not a neanderthaloid and should be placed in the earlier Neanthropidæ group described later.

The Steinheim skull may also have resembled the Krapina and Ehringsdorf skulls in some morphological details and some human evolutionists have concluded that these remains represent an early branch of the neanderthaloid stock distinct from a later branch consisting of the remaining types. This earlier stock seems to have been more human in appearance and in general characters and this may mean that the other and later stock developed along its own lines leading away from the *Homo sapiens* type. If this is true, it also means that modern man is not descended from the later neanderthaloid stock. Le Gros Clark² expressed this point well. He stated that by a progressive development of the *Pithecanthropus* type of man a generalized Neanderthal type was eventually produced which led to two separate lines of evolution. In one line, the line continued to develop but in conjunction with exaggerated eyebrow ridges, exaggerated development of the jaws and palate, specialization of the teeth and changes in the limb bones reminiscent of lower types leading to the more typical neanderthaloid. In the other line, the brain also developed, but the eyebrow ridges became smaller, the jaws became less prognathous and the teeth smaller and the skull became more rounded, while the limb bones kept their human-like appearance. Eventually this type produced *Homo sapiens*. Such a line could lead, of course, through a type like *H. steinheimensis*.

These neanderthaloid fossil remains thus present a mixture of characters which in some cases are pithecanthropic, and in others approach the *sapiens* type still further. The combination of these characters varies; for example, the later neanderthaloids possessed a pithecanthropic skull, but the brain was very large and the femur curved unlike that of the older *Pithecanthropi*. On the other

¹ 1933, pp. 63-64.

² 1930, p. 104.

hand, the Steinheim skull had a small brain but a more *sapient* appearance. There is a modern tendency to group the earlier *Pithecanthropus* types, the Neanderthal forms and Rhodesian man together as the Palaeoanthropidae because they resemble each other in a greater number of characters than they resemble Palaeolithic or modern man.¹ Zuckerman defined and summed up the skull features of the group which also shows their relationships well. He wrote:

The main characteristics of the skulls of palaeoanthropic man can be simply stated. While having roughly the same overall dimensions as those of modern or neanthropic man, they are differentiated by having low sloping foreheads and small and flattened sagittal areas, a characteristic to some extent indicative of an unexpanded vault. They are furnished with strong eyebrow ridges and their cranial muscular markings are in general more pronounced than those of modern man. The occipital region is usually very wide, the maximum width being found in the mastoid region as in adult apes, and is bent at an angle to the rest, shelving sharply into the neck to which it was attached by a powerful musculature. The face is prognathous and the chin poor, if at all developed. Cranial capacity in the Palaeoanthropidae varies between 755 and 1625 cc., as compared with an established range of from 900 to 2100 cc. with an average of about 1500 cc.² in modern man. The average capacity of some eight *Sivapithecus* skulls is 940 cc.,³ and of four skulls of *Pithecanthropus erectus* is about 860 cc.⁴ There is no overlap between the ranges for cranial capacity in man and apes, the largest ape skull yet recorded having a capacity of only about 675 cc.⁵

b. The Neanthropidae

(i) *The earlier Neanthropidae*. This group also falls into divisions based on age. The earlier fossils consist only of the two types, the Swanscombe skull and Fontéchevade man.

In 1935 a most interesting discovery was made by A. T. Marston⁶ in a gravel pit at Swanscombe in Kent. He found a parietal and an occipital bone. Unfortunately, the facial bones were missing, but those found were very well preserved and the sutures were little damaged so that they could be placed in their correct position and compared with modern skulls perfectly. It is agreed

¹ Zuckerman, 1950, p. 439. ² MacDonell, 1904.

³ Weidenreich, 1943. ⁴ Weidenreich, 1945.

⁵ In this final statement it is implied that the Australopithecines are not hominids.

⁶ 1937.

among human evolutionists that these bones were part of a human skull little distinguishable from the skull of modern man, although the bones are decidedly thicker than modern skull bones (see Plate 15).

The cranial capacity was probably in the region of 1300 cc. and the brain markings as shown by endocasts were also complicated, just as in modern man. Unfortunately, in the absence of a mandible and the face region, we can never be sure about the appearance of the complete skull. The important feature about this discovery is the fact that its age can be determined with certainty. Associated with it in the gravel beds were flint implements of the characteristic Middle Acheulian type and also some bones of red deer, an elephant and *rhinoceros*. The fluorine content of the skull was determined at 2 per cent. These findings place the date of the skull in the Middle Pleistocene about 250,000 to 300,000 years ago. The absence of the face region does not preclude the conclusion that the Swanscombe skull belonged to a human being perhaps not a great deal different to *Homo sapiens*, and thus the skull is an undoubted indication that human beings of advanced type have been in existence much longer than we would expect from the other advanced known fossil material. Swanscombe man may be much older than the neanderthaloids and was certainly contemporaneous with them.

In 1947 another interesting discovery was made by Mme. Henri-Martin from a cave at Fontéchevade and was described by H. V. Vallois.¹ This discovery comprised most of the parietals and the upper part of the frontal bone of one skull, and the frontal bone of another skull. These skull bones were also very human in appearance and were like those of modern man, but their thickness resembled that of the Swanscombe skull. In width it also resembled this skull. The capacity has been estimated at about 1450 cc. The forehead was vertical and there were no large eyebrows, or visor, and hence this creature does not resemble the Neanderthal type. These fossils date from the beginning of the Riss-Würm (last) interglacial period, that is, they are at the beginning of the Upper Pleistocene about 150,000 years ago, or perhaps they date from the Middle Pleistocene. Implements of the Tayacian type were found in the same deposits as these fossils, which together are called Fontéchevade man.

¹ 1949.

The Kanam fragment should be mentioned here. This consists of a lower mandible with a chin. It was found at Kanam, near Lake Victoria in Africa. Other African pieces of skull bones have been found which are all considered to be of early Acheulian age (i.e., Lower Middle Pleistocene), but insufficient pieces have been so far discovered to generalize any further than admit the possibility of the presence of modern man in Africa at this early period as well as in Europe.

The infamous Piltdown remains should also be mentioned. The discovery of Piltdown man (*Eoanthropus dawsoni*) was heralded with great publicity and great names such as those of Smith Woodward and Teilhard de Chardin were associated with it. The bones consisted of skull fragments, teeth and a mandible of Early Upper Pleistocene age. The circumstances of their discovery strongly suggested that the bones were those of one type, but, unfortunately, as J. S. Weiner *et al.*¹ showed, a large element of fraud entered into the matter which was not connected to the people whose names are mentioned above. It appears that the mandible and teeth were deliberately faked. They are in fact those of a modern ape altered to give an impression of age and affinity with the other truly older parts of the cranium. Under these circumstances suspicion must attach to all the findings, and perhaps it is better to exclude them from consideration. The cranial fragments, however, are of human type and their age is Early Upper Pleistocene. It should be stated that *Eoanthropus dawsoni* had always been something of an enigma to many anthropologists because of the unusual association of simian and human characters in them and many people refused to accept them at their face value. An excellent concise short review of these bones was given by W. L. Straus, Jr.²

(ii) *Homo sapiens*. About 100,000 years ago, in the middle of the Upper Pleistocene Period, the Mousterian or Middle Palaeolithic Cultural Period came to an end, and was succeeded by the Upper Palaeolithic Culture comprising those types called Aurignacian, Solutrean and Magdalenian, each characterized by their own distinctive brand of industry. In Europe at any rate, Neanderthal man died out completely and was replaced by these later Palaeolithic types. The fossils which have been found belonging to the group include those from Cro-Magnon, Grimaldi, Pred-

¹ 1933. ² 1934.

mont, Brunii, Combe-Capelle and other European places. Wadjak man is a late type found in Java which resembles the modern Australian aborigines. All of these fossil men would merely seem to be varieties of *Homo sapiens*, differing only in features such as prognathism, which in Cro-Magnon man, for example, was more pronounced than in present day man, but very much less than in the neanderthaloid types. There is no need to describe these forms of man further, especially as their racial relationships are rather obscure. In the evolutionary sense they were fully developed specimens of the human race.

D. The lineage of man

With the description of the evolution of man the factual account of evolution which we have given in previous chapters becomes complete. As already pointed out, there is no scientific doubt that man belongs to the order of Primates, and although there are many gaps between the various groups of animals involved in an evolutionary scheme, there is still a large amount of evidence from comparative anatomy, etc., which points the way to the evolution of the Primates from lower animals. Different workers may have different schemes differing in details. Le Gros Clark¹ gave a general scheme somewhat as follows: at the end of the Mesozoic Period a basal stock of generalized placental mammals evolved, and the various orders of higher mammals sprang from it. Among these orders there was one from which the Primates evolved. This group may be referred to as the Basal Primates. From this stock arose two groups, the Protolemuroids and the Prototarsioids, in Palaeocene times, and also very early on arose the Anthropoidea or Pithecoidea from which all the monkeys, anthropoids and hominids developed. Two Eocene fossil forms called *Amphipithecus* and *Aleaticopithecus* are sometimes looked upon as the stock from which the Old World Primates came.

It is generally agreed nowadays that man could not have evolved from any of the existing ape groups. But, excluding mental characteristics, which are not comparable, the two groups of man and apes are very close together. Man is specialized in the direction of his brain and is upright, while the ape group is

¹ 1934, pp. 222-226.

specialized towards brachiating (i.e., they are arboreal creatures able to swing from branch to branch in the forests). This is not to say that all modern anthropoids are brachiators—the gorilla, for example, seldom seems to leave the ground. The two groups are so phylogenetically close to each other that a common ancestor sufficiently generalized could have given rise to both man and apes. Such a descent could take place in various ways and Figure 25 shows three chief ways in which it might have occurred. In A

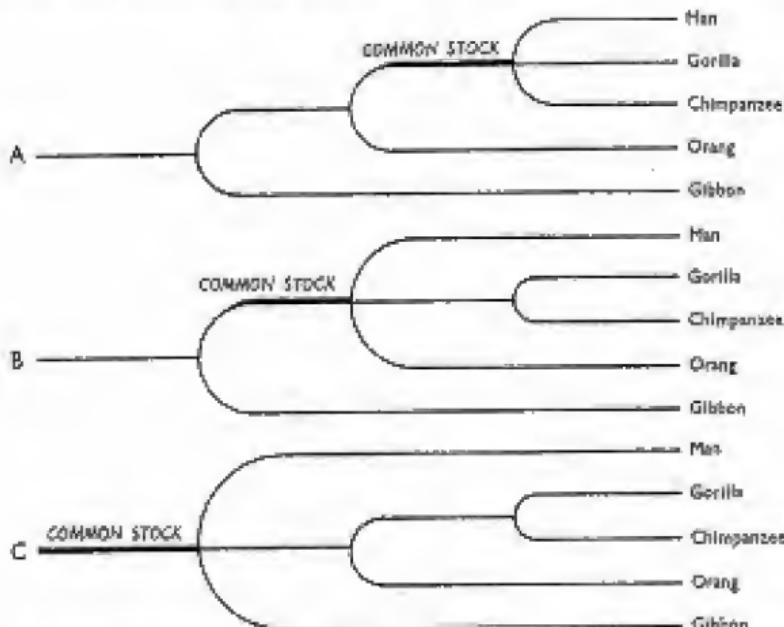


Fig. 25. Diagrams illustrating variations of the common-stock theory of human ancestry. (After F. W. Jones, 1929.)

a common stock is visualized as giving rise to man, gorilla and chimpanzee; in B a common stock gave rise to these three and also the orang; while in C the common stock produced man independently of the others. In these schemes it may be noted that the age and ancestry of man is pushed back further into the past from A to C. It is true that as more and more hominid fossils are discovered, the existence of man in earlier times becomes evident. The discovery of the Swanscombe skull and Fontéchevade man illustrate this point well. As Zuckerman¹ so aptly said: 'The

¹ 1933, p. 178.

available evidence cannot even deny the possibility of man's independent evolution from as far back as the Oligocene, and through the Miocene up to the present day.¹ The oldest member of the genus *Pithecanthropus* appeared at the beginning of the Lower Middle Pleistocene, but, of course, he must have had ancestors previous to that Period. The discovery of Tertiary man would be an event of outstanding importance.

In the earlier days of the study of human evolution it was simple to visualize an evolutionary scheme in the form of ape—*Pithecanthropus*—Neanderthal man—modern man. No doubt there was a large hiatus between ape and *Pithecanthropus*, but the scheme seemed to be possible and further investigations could reasonably be expected to fill in the gaps. Human remains begin abruptly with *Pithecanthropus* and up to the present no sign of earlier types has appeared. Although *Pithecanthropus* is ape-like to some extent it is so different from anthropoids as to preclude a direct connection. Apes and monkeys of all kinds appear from the Tertiary Period onwards, but there is no sign of man in that Period. The great interest of the Australopithecinae lies in the fact that they seem to bridge this gap between ape and *Pithecanthropus* type both morphologically and geologically. Thus there is some evidence to connect the earliest hominids with the earliest ape stock which means that the Pongidae and the Hominidae may have arisen from a common ancestor or ancestors. But the evidence showing that *Australopithecus* was a human being is still perhaps too small to be definite about.

When we come to the hominid fossils themselves, excluding *Australopithecus* which some anthropologists consider to be hominid, the picture of human evolution is still not too clear. From the apes, through the *Pithecanthropus* series up to *Homo sapiens* there is an overall increase in brain capacity in that order which suggests the evolutionary direction, and there are other examples of similar trends. The neanderthaloids here, with their beetled brows, prognathous jaws and large brains present at a relatively late date, are perhaps anomalous. It is a fact commonly admitted that the neanderthaloids did not give rise to *Homo sapiens*, but that they form a side branch from an earlier stem. We may again mention Le Gros Clark's¹ view already given on page 277 in which he visualized two lines of evolution from the

¹ 1930.

Pithecanthropus type, which, of course, supports his later recognition of only two species in the genus *Homo*, namely, *H. neanderthalensis* and *H. sapiens*.¹ An interesting evolutionary series was given by Weidenreich² in which he considered that giant hominids evolved to present-day man in the order: *Meganthropus*—*Pithecanthropus robustus*—*Homo soloensis*—Wadjak man—Australian aborigine. But this is a speculation which has been criticized by other people. Indeed, the discovery of the infant skull called *P. modjokertensis*, which is older than *Meganthropus*, contradicts Weidenreich's view. There are other opinions about the lineage of man.

Our survey has attempted to bring out the facts relating to the evolution of man which are fairly clear. If we grant the position of Solo man as an advanced member of the genus *Pithecanthropus*, then the hominid fossils suggest three more or less distinct types, or better still, levels, of evolutionary progress: (a) the *Pithecanthropus* series consisting of *heidelbergensis*, *modjokertensis*, *pekinensis*, *erectus*, *soloensis* and perhaps *Atlanthropus*; (b) the neanderthaloids; and (c) *Homo sapiens*, consisting of Swanscombe man, Fontéchevade man, Palaeolithic and modern man. Within their types each of these are distinctly related, but the connections between the types are not as yet clear, and we await the discovery of more material. The important point about these fossil hominids, as Humphrey Johnson³ pointed out, is that while a few decades ago man stood alone in the animal world, today this is by no means the case. All the scientific evidence derived from palaeontology, comparative anatomy, morphology, physiology, etc., show distinctly that since about half a million years ago several types of man have come into existence and have died out. The kinship of man on the physical level with other animals, while not absolutely established, is much clearer than it was. True men were already diversified in Early Quaternary Times. J. S. Weiner⁴ has recently illustrated these different types of men in relation to their age, their cultural advancement and their increasing likeness to modern man. His diagram is reproduced in Figure 26 which also illustrates the chief points we have been attempting to make in this account of human evolution. The chief feature to notice about this diagram is that in it Weiner derives all the known human types from the single stock of *Pithecanthropus*.

¹ 1935.

² 1945.

³ 1956, No. 2.

⁴ 1959.

EVOLUTION AND CHRISTIANS

Le Gros Clark¹ summed up the situation fairly when he wrote:

In considering the palaeontological background of human evolution (and also of the evolution of the anthropoid apes) it is necessary to give more attention to the fact that it has been complicated by quite a remarkable diversity of evolutionary radiations in the past and, in so far as the new fossil evidence indicates that collateral lines of

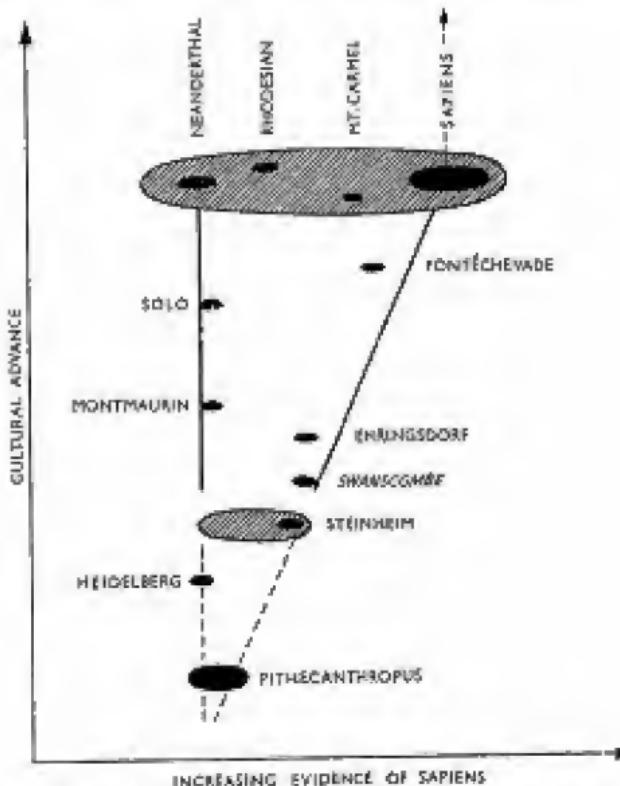


Fig. 26. The phyletic lineage of the various hominid levels in terms of cultural status and increasingly sapiens type. (After Weiner, 1939.)

evolution have been relatively numerous, it can only accentuate the need for caution in seeking to interpret the precise phylogenetic relationships between fossil types and modern types. In general, it may be said that more complete palaeontological sequences are required before such relationships can be established with any degree of confidence.

¹ 1939.

This quotation brings us back to the point with which we started in this section, namely, that it is generally accepted by competent authorities that physical man has evolved from some lower group of animals, but how this evolution had occurred, or from what group (except remotely), is unknown. It should be pointed out that the question of the evolution of man's body is a scientific question and it can only be determined finally by scientific means. It is a question that has arisen within the bounds of biological and anthropological science as knowledge of physical man and of other animate creatures increased. The question is not by any means settled; as a scientific problem it is still a matter for scientific consideration. Philosophy only takes up from science when the scientific problems are solved or nearly so, that is, when they are no longer problems. But in the meantime the possibility of the solution of the scientific problem should be realized and therefore its implications discussed.

A very important question arises from these fossil hominids. It is: 'Were all these creatures human beings, that is, men with a spiritual immortal soul?' It may be taken for granted that if an ancient skull indistinguishable from that of present-day man were discovered, then the possessor had been a human being as we know him. The Swanscombe skull is possibly the nearest approach to this, but unfortunately it is not complete. The majority of the earlier hominids present characters unmistakably human but also characters suggestive of apes. Other evidence is needed before it can be decided whether the possessors of these bones were true human beings.

This evidence is intimately bound up with the question of the fundamental difference between man and animal. The consideration of this difference would take us deep into the realms of philosophical psychology and related subjects. It is in fact a very abstruse matter beyond our terms of reference. No Christian needs to be assured that there is a vast impassable gulf between the mind of man and the 'mind' of any animal no matter what its state of development. This is commonly expressed by saying that man is a rational creature (the *animal rationalis* of the scholastics), while an animal is not. This is not to say that animals do not possess some form of 'intelligence', but it implies that there is a difference in kind between the human and animal intelligence. We cannot go much further into the matter here, but readers who

wish to pursue it further will find an excellent account in J. Doneel's *Philosophical Psychology*¹ with references. Suffice it to say that man's reason, or rational intelligence, is able to reflect upon itself. Man is conscious of being 'I', and hence he can appreciate those concepts the philosopher calls universals; he can understand the true relations between things and so on. In other words, he has the power of abstraction, of forming ideas, and he can communicate these ideas to his fellow men. Man can talk, and his speech is not just due to a certain arrangement of his vocal chords, although these are the physical pre-requisites for speech. Man can make machines to do work better than he can himself. Man develops a culture based on his knowledge and ideas, and it is passed on from generation to generation by tradition and communication. These are all qualities of his human spiritual soul which are possessed by no animal. In fact it is inconceivable to picture an animal with these qualities.

The possession of these qualities by human beings leads to activities which are uniquely human, and it is these activities (or some of them) which provide the evidence for the determination of the rationality, and hence truly human status, of the fossil hominids. These activities provide the basis of the Palaeolithic cultures studied by the anthropologists. Important Palaeolithic activities, or industries, are those of tool-making and using fire, burying the dead ceremoniously, and, in later times, making drawings and crude sculpturings or other forms of art. The reader will find a fine concise account of some of these activities in K. P. Oakley's *Man the Toolmaker*.² Such activities imply the use of human reason, and it is well known that these industries began in a simple way, particularly regarding the tools, and as man gained knowledge and experience, they changed always for the better. The materials used for tool making were wood, bone, shell, stone and lastly metal; while the Palaeolithic industries passed through the cultures represented by pebble tools, hand axes, chopper tools, flake tools to blade tools.

As regards the early hominids, no implements of any kind were found associated with *Pithecanthropus erectus*; but with his Chinese relation, *P. pekinensis*, roughly shaped pieces of various rocks were found, some of which may have been used as choppers, and others were pointed or blade-like. In the Choukoutien caves charred

¹ 1955. ² 1950.

animal bones and the remains of hearths were also found, indicating that *Pithecanthropus* in China knew the use of fire. These activities have been fully described by the Abbé Breuil¹ and Teilhard de Chardin and Pei.² Vallois³ discussed the position of *Pithecanthropus* and *Sinanthropus* and concluded they were exactly intermediate in many respects between man and ape. Because of their primitiveness, however, he preferred to call them *prehominids* rather than *hominids*. We may note that there is some evidence to show that *Australopithecus* made and used tools.⁴

It now appears that Rhodesian man made flake tools, shaped bone tools and made stone balls, but the tools found near the Rhodesian man deposit may be fairly recent. Acheulian flint hand axes were found with Swanscombe man, and primitive Tayacian implements were associated with Fontéchevade man. *P. heidelbergensis* may have known the use of implements because, although none were found with the jaw, pieces of bone which seemingly had been deliberately fashioned were found in the same beds. No implements were found with the Steinheim skull, but Mousterian tools were found with the Ehringsdorf skull. No tools have been associated with Solo man. Finally Neanderthal man had considerable knowledge of toolmaking (Mousterian level). He used fire and he buried his dead ceremonially. The fossil hominids then from *Pithecanthropus pekinensis* upwards (and *P. erectus* must be included with this form because of morphological resemblances) show evidence of the use of reason. Some anthropologists have contended that highly developed animals could copy the use of fire, or make use of fire already started by some natural means, and that they could even use stones as implements. But these points would require strong scientific support before they could be accepted as even possible. In any case no animal in nature however highly developed could conceivably shape a piece of bone or rock for a specific future purpose.

It should be remembered also that, independently of the fossil hominid remains, anthropologists recognize the Palaeolithic Culture Period which started in the middle of the Lower Pleistocene from the end of the First Glacial Period. Various implements found in different geological strata have indicated the industries which we have already noted; starting from the Lower Palaeolithic they are: Abbevillian, Acheulian, Mousterian,

¹ 1931 and 1935. ² 1932. ³ 1937, pp. 142-146. ⁴ See p. 262.

Aurignacian, Solutrian and Magdalenian Periods, which represent different and increasingly more human cultural levels. The presence of implements as old as the Abbevillian and onwards is evidence of the presence of rational men in those times. The association of definite implements with some of the fossil hominids and his use of fire when known is confirmatory evidence that men existed during those periods of the Pleistocene. Thus it seems generally agreed among evolutionists and anthropologists that the fossil hominids were men.

A consideration then arises from the nomenclature of the hominids. There has been a tendency to erect new species and even new genera whenever a new fossil was found if it showed differences from known fossils. The best example was Black's naming of Pekin man as *Sinanthropus*, that is, a new genus which was done on the basis of a single tooth. Fortunately, many other bones were found later which were referable to *Sinanthropus*, and this form was then shown to be a true hominid. Further investigations have shown that there are no real differences between *Sinanthropus* and *Pithecanthropus* great enough to justify the creation of separate genera for them, and it is doubtful even if they were separate species.

The naming of these fossils is in fact arbitrary and often a matter of convenience. But as more and more of them become available the classification will become clearer. Nevertheless, the question of nomenclature is widely discussed among human evolutionists. The present rather indiscriminate method is not satisfactory to anyone, but some of the difficulties seem to arise from the fact that anthropologists are not necessarily systematists in the biological sense. At a Cold Spring Harbor Symposium on the evolution of man in 1950, Mayr, as a foremost systematist, was asked to give his opinions about the classification of the fossil hominids and near-hominids. He concluded there is no evidence that more than one species of hominid ever existed at any given time. And he proposed to classify fossil and recent hominids into one single genus, *Homo*, with three species, namely, *transvaalensis*, *erectus* and *sapiens*. There may be sub-species, and Mayr considered that man's versatility and his slowness in becoming reproductively isolated have prevented him from splitting up into more species.¹ We note here that the Australopiths (*transvaalensis*) are included.

¹ 1950, pp. 109-118.

If these were not true hominids then there would only be two species in the genus. *Homo erectus* is represented by Java and Pekin man; while the species *Homo sapiens* included the three sub-species modern man, Neanderthal man, and pre-Neanderthal man. At the symposium at which this simplified classification was proposed, it was largely welcomed. Even with a simplified classification it still appears that there are different levels of hominids sufficient to warrant the recognition of distinct species of *Homo*. Thus the question of the importance of the possibility of different levels of men arises in philosophy and theology. An answer, of course, hinges on the meaning of the word 'species' in biology. We have already indicated in a previous chapter the difficulties surrounding precise definition of this word, although no biologist doubts the actual existence of such natural categories. The process of evolution in itself, however, is an important factor limiting the distinction between closely related species. In any definition given there will always be borderline cases and species grading into species because of evolution and of the genetic mechanisms involved in the reproduction of individuals.

Taking the idea of species as it is accepted by biologists we may well ask does it matter as far as man is concerned? This question does not belittle the biological concept in any way, but from a theological and philosophical point of view, as long as a creature is able to reason in the human sense as distinct from the possession of mere animal intelligence, or has the potentiality to reason, then that creature may be regarded as a human being. It is the mental and spiritual qualities which make man what he is. It is these that decide his nature to an immeasurably greater extent than his structural characters.

These qualities may be summed up by saying that human beings are able to reflect. In the evolutionary sense the change from animal to human was described by Teilhard de Chardin as crossing the threshold of reflection. He calls this process *hominisation*, or an instantaneous and individual 'leap from instinct to thought'. Teilhard would seem to imply that this change or crossing of the threshold of reflection could only occur once, and that at the very beginning of the human stem. The ancient forms of fossil men, such as *Pithecanthropus*, sometimes called pre-hominids as we have already noted, are therefore fully human from the first moment of their appearance. Thus there can be no true link between a lower

animal and a creature who has crossed the threshold of thought, except perhaps structurally. As Teilhard wrote:

A mutation therefore as fundamental as that of thought, a mutation which gives its specific impetus to the whole human group, could not in my opinion have appeared half-way up the stalk. It dominates the whole edifice. Its place must therefore be *beneath* every recognizable verticil in the unattainable depths of the peduncle, and thus beneath those creatures which (however pre-hominid in cranial structure) are already clearly situated *above* the point of origin and blossoming of the race.¹

By peduncle and verticil here Teilhard simply means the human stem and its branches or levels.

There is no overlap in brain capacity, and hence as far as we can tell in mental capabilities, between any known anthropoids and any known hominids. This statement, however, is only true if *Australopithecus* is excluded from the family Hominidae. But, although the brain of *Australopithecus* was little larger than that of an ape, it could have been much more complicated and developed in proportion and there are some indications to this effect. If, however, we accept *Pithecanthropus* as being human, then man appeared 'suddenly' in the Pleistocene Era.² Such is the difference between *Pithecanthropus* as indicated by his cranial capacity, that there is no biological reason to expect such an increase in brain size to have occurred more than once. In the biological sense alone a change of this kind is immense, and all evolutionary knowledge indicates that such major changes are not repeated. They occur once and for all; the conditions bringing about their further production are rarely repeated. The change which produced a creature capable of being a human being is at the very least on a par with the kind of changes which produced the various phyla, and no biologist has ever suggested that even fishes, birds, higher vertebrates, etc., let alone phyla, have been produced over and over again. There are then strong *a priori* reasons, and strong biological probabilities, to suppose that man has appeared once

¹ 1959, Book 3, Chaps. 1 and 2, and pages 194-195. The word 'bienialisation' was coined by Teilhard de Chardin to express the attainment of the power of reflection, etc.

² That is, on the evidence presented by the hominid fossils. We must remember that, as knowledge of the recently discovered *Oreopithecus* increases, the age of man will probably be found to be much older than that which we can infer from the *Pithecanthropus* remains.

only in the evolutionary scheme. Vallois¹ considered that all the known hominids have undoubtedly had a monophyletic origin. While Arambourg² considered that speculations on polygenism are out-moded. Le Gros Clark³ allowed for the possibility of polyphyletic origin of different races of men but he thought that 'it is perhaps not very probable'. According to Teilhard de Chardin (1939) the problem of monogenism, strictly speaking, *shades* science by its very nature. This applies with greatest force to the study of the fossil men who always appear in a 'crowd', as it were. The problem of monogenism may, however, be speculated on in a genetical sense.

Granted his initial appearance, relatively small-brained but still human, there seems to be no reason in the early stages of his appearance, when his animal potentialities and his newly acquired status were strongly asserting themselves, why he should not develop still further mentally and physically up to a maximum point beyond which he could not go unless some further major change occurred in his brain which would be at least as large as the change which led to his production. It is worth pointing out that, although modern man has done many very wonderful things and has produced many supreme literary works, there is no evidence that modern man is any more innately *intelligent* than the first man. No one can really say that Einstein or Aquinas were more or less intelligent than Aristotle or Plato, or Moses, or the man who made the first wheel or the first implement.

We mentioned at the beginning of this chapter that man is unique, and without doubt he is the end point of evolution at the present day. There are many biological reasons for believing that major evolutionary changes have ceased, that is, that major evolution is at an end. Not least among these reasons is the fact that the evolutionary lines we already know about have led, or are leading, to increasing specialization along limited paths which, as evolution teaches, leads sooner or later to extinction of those lines. This has been realized by eminent biological authorities such as Sir Julian Huxley and others, and it is a point which Huxley recently made to the general public in the *Sunday Times*.⁴ Man, however, except for his brain, is not particularly specialized structurally—in fact he is generally regarded as being a generalized

¹ 1930, p. 81. ² 1948, p. 143, and see J. O'Neill, 1939, Part 2.

³ 1915, p. 79. ⁴ 1953.

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kind of animal, and he is the dominant animal on earth. His brain enables him to maintain his dominance, and to ensure for himself a continuance of his kind and to see that no lesser creature supersedes him. His only danger is one of deliberate self-extinction. A further evolution of his body in any major respect would mean biological over-specialization and hence ultimate extinction, and he could possibly prevent this tragedy unless he destroyed himself first.

It may be said, therefore, that evolution of physical man has ceased for all practical purposes, but he may still evolve to a certain extent in his mental capabilities, but even this would seem to be limited. Later, in the last chapter, we will suggest that the evolution of physical man has stopped for another reason, and that his future evolution lies along a different plane, if indeed it can be called evolution, strictly speaking. By this we mean the pursuit towards his true end.

Chapter VIII

Evolution and Christians, Continued

I. EVOLUTION AND THEOLOGY

1. General Account

In this and the following section I am not attempting to consider evolutionary theory in relation to Christian thought in general. This would be a very large task because of the wide divergence of opinion among non-Catholic authorities both as regards their attitude to evolution and to the Christian religion. I am here looking at evolution from the Catholic viewpoint, but there should be much in it of interest to non-Catholics. Readers who wish for a good short general account should consult David Lack's *Evolutionary Theory and Christian Belief* which also contains references to other works.¹

If we accept the physical origin of man's body from the brute creation, then clearly this is a matter which is bound to touch the Christian Faith at several points. The central pivots of our Faith are the Incarnation and the Redemption of man by Christ. The Redemption is a fact; it is an event which took place at a point in human history and its effects will continue as long as there are men to be redeemed. There could have been no Redemption unless the necessity for it arose and thus the Redemption presupposes the Fall and original sin. Catholic teaching, based on Genesis, holds it as of Faith that original sin was an actual sin committed by the first man, or Adam, in disobedience to God's plain command. By it Adam lost his special position in the world and his special gifts, but most of all he lost his chance 'to walk with God' eternally. God had given Adam the opportunity to attain heaven

¹ There is not a large, easily accessible, Catholic literature on the evolution of man and theology. A choice is given: Begouen, 1945; Bone, 1947; Boyer, 1947; Brien, 1932; Dordalot, 1923; Hauret, 1930; Hedley, 1937; Johnson, 1923, 1947; Marconi, 1948; Messenger, 1931, 1949, 1954; O'Neill, 1939; Renic, 1930; Teilhard de Chardin, 1948. Some non-Catholic accounts are given by: Lack, 1957; Raven, 1943, 1953; Smethurst, 1955; Coulson, 1951; Webster, 1932; B.B.C. Symposium, 1930; Paton, 1935; Mascall, 1956, etc.

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but original sin deprived him of this opportunity. The gravity of Adam's offence is seen the more when we realize that, although to Adam it was an actual sin, the guilt incurred was so monstrous that it affected the whole human creation. All Adam's descendants, although they have committed no actual sin, fall under this guilt—all men are born with the stain of original sin on their souls, as it is expressed. Before Adam and man can see God they must be cleansed from the effects of this sin by Baptism which enables them to merit the effects of the Redemption.

These, of course, are facts which we know by Faith and the infallible teaching of the Church instituted by Christ. They are facts which have been taught by, or were implied by the teaching of, the Church since its inception, and were implicit too under the Judaic Dispensation when the hope of the coming of the Messiah was still vivid among the Chosen People. A Christian knows all this, and sees no reason to consider it otherwise than as basic to his whole conception of his relation to God, his Creator. Such truths of Faith are truths in the absolute sense because they are revealed by God—and this is possibly the only way in which we may know absolute truth. There should be no outstanding difference between the interpretation which a Catholic will give to evolution, particularly the evolution of man, and many other non-Catholic, but Christian, interpretations, in which the full force of the Redemption is recognized. The fact that God became Man at a certain point in human history affects the whole of one's attitude to life and its ramifications, and determines our understanding of the nature of man which is denied to those who do not believe in the Incarnation and the Redemption.

If, then, any scientific finding of whatever kind truly contradicts the basic truths of Christianity, something is wrong, and seriously wrong. Our Faith can never be wrong; hence, at first sight, it would seem that the scientific finding is wrong. But the scientist is also a man who seeks after truth, using his God-given reason to attain it. It often happens, however, that the scientific finding is plausible, easy to grasp, and produces manifold practical effects. The inevitable result is that the force, or impact, of the religious truth affected is lessened in its effects upon people. It is not so much that people, by and large, deliberately say that such and such scientific facts contradict, or do away with, the necessity for, such and such religious doctrines, as that the accumulative

effect of scientific teachings when presented in certain ways destroy the *milieu* in which Faith can grow and be nourished. And this effect of science is made even worse when its findings are used as propaganda to attack and undermine religion. Hence it is that the Catholic Church is very careful and discerning when new scientific discoveries which may possibly touch on religion become available, because it is the business and *raison d'être* of the Church to promulgate and preserve the Faith, to protect it from error, and to protect her members from error which may in any way weaken their chances of attaining their end, which is to see God. To a Catholic this end is the most important thing of all. In the perfect order of things all should tend to this end.

As we have already indicated in Chapter 1 deeper examination of contradictions often shows, however, that neither the Church nor science is necessarily wrong. True science should not oppose religion and religion need not oppose science. As we mentioned in Chapter 1 antagonism between science and religion is only an apparent antagonism. It is real enough in the sense that there is a problem to be solved, but its reality is only transient, unless indeed propaganda prevents any resolution of the matter. Both the theologian and the scientist experience a compulsion which drives them on to pursue their chosen tasks. Both expect their serious ideas and conclusions to be treated with the respect they deserve. But, alas, the history of the last hundred years alone has shown that this respect, this consideration for others, has often been lacking in large measure on both sides. Antagonism was inevitable and it was often fanned by the biased pen of the propagandist.

The story of the development and reception of the evolution theory gives us one of the best examples of this antagonism which we now know need never have been. As regards evolution and science in general, the effect has been disastrous—the propagandist has ensured the successful appreciation of science to ordinary people without bothering much about their fundamental understanding of it, especially in relation to religion. Nowadays it is only too true that one need only say that science proves something (whether it does or not is immaterial) and many people will accept it as true without further consideration. To say that something or some statement is 'unscientific' is equivalent nowadays to saying it is wrong and couldn't possibly be right. And by science

here is meant only empirical or positive science. As a result even deeply held convictions may be thrown over because, it is said, science teaches the opposite. It is an amazing experience to question students at a university level about science and philosophy or theology. To many science students at least, science is truth, science cannot err, science is a god; while philosophy and theology are just nebulous talking shops allowing certain types of persons to exercise their intellects, but of no fundamental value. Unfortunately many of these students become the future teachers and researchers of science and the error is perpetuated.

Fortunately there are signs of change in this unhealthy attitude which is so largely due to misunderstanding of the true positions of all the sciences in the hierarchy of knowledge. The lack of a realization that each branch of science, taking the word in its broad meaning to cover all aspects of knowledge, has its limitations and limits beyond which it is not competent to go, has helped greatly to produce this overall dominance of science, taken in the narrow modern sense. The solution to the impasse, which perhaps is already taking place, is obvious; it is that a true synthesis of knowledge can only come about by co-operation between people pursuing all the various branches of knowledge. All the positive sciences can give much of value to those of philosophy and theology, and these in their turn can synthesize scientific knowledge, pointing out the pitfalls and checking errors. But co-operation implies respect, and there can be no respect in an atmosphere of antagonism. Controversy and discussion are vital to the progress of any branch of knowledge, but what can be the result if, to take an extreme and fictitious example, a clergyman comes along and says to a geologist, 'The Bible *proves* the world is only 6,000 years old.' And the geologist says, 'Nonsense, geology *proves* that it is millions of years old.' 'There you are,' says the clergyman, 'science is contradicting the Bible; science is attacking religion; all you scientists are atheists.' 'Pooh!' says the geologist, who is a church-going man himself. 'If what you say about the Bible is true, then the Bible is just a collection of fairy stories.'

Such a conversation may sound ridiculous, but yet it represents the sort of thing that has happened over and over again in the past hundred years and still happens yet. Both the clergyman and the geologist show their ignorance, and what could have turned out

to be a valuable discussion on the age of the earth merely became a scrapping match in which both contestants were the losers. The result of such approaches to varying branches of knowledge as exemplified by these two imaginary and pompous people is antagonism. There will be no synthesis there.

Pope Pius XII realized the futility of this impasse years ago and in many excellent counsels¹ he encouraged priests to study science sympathetically—it is dangerous to be ignorant in the face of modern scientific knowledge; he encouraged scientists of all kinds to pursue their legitimate tasks; he encouraged philosophers and theologians to examine the conclusions of science; and he invited all to unite and pool their knowledge to attain a universal synthesis for the good of mankind. But the Pope was careful to point out that there comes a stage in scientific reasonings beyond which science cannot go, and it is at this stage that 'the guiding light of philosophy' is needed to illumine men's minds further.

And now a spirit of co-operation is in the air. In the first of a series of articles on 'The Destiny of Man' in the *Sunday Times*² Sir Julian Huxley, who is one of the most eruditè of living evolutionists, has reached the most important conclusion, based on his biological studies, that man is indeed a 'new and unique kind of organism', who has 'stepped over the threshold of a quite new phase or sector of the evolutionary process. We call it the human or psycho-social phase'. Huxley considered man to be the sole representative of a new realm of beings whose importance transcends that of all the animal kingdom together. He suggested the name *Psychozoa* for this type of being. Evolution has shown the importance of the study of the nature of man which Sir Julian sees only as directed effectively towards his psycho-social aspects, that is, towards his mental (and spiritual) attributes. He wrote: 'The time is now ripe for an intensive and scientific study of psycho-social evolution and the possibilities and limitations of mankind.'

This article embodied a welcome recognition that man's intellectual spiritual soul, as the Catholic philosopher would say, is that which determines the nature of man. Such a recognition cries out for co-operation and indeed in a later article in the same series Father Corbishley³ recognized that Huxley's article and his

¹ 1935, 1941, 1950, 1955, etc.

² *Sunday Times*, 15 July, 1958.

³ *Sunday Times*, 17 August 1958.

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statements provided real points of contact of the biologists with other disciplines. He wrote: 'But Sir Julian is no narrow scientific bigot. His honesty of mind and generosity of purpose are potent and his article may well prove to be a turning-point in the relations between biologists and theologians who, since the publication of *The Origin of Species*, have scarcely been on speaking terms.' Corbishley pointed out that this term 'psycho-social' may be very misleading. Indeed Huxley did consider in general that the principles of biological evolution as such should be a guiding mentor in the study of this further phase of evolution. Such counsels are wise and correct and may lead to fruitful results if the researches involved follow a true line respecting the dignity of man as a unique and spiritual being. Equally we may say that evolutionary science is approaching the point beyond which it may not usefully go without the help of disciplines concerned directly with the nature of man as a spiritual being.

Religion has been the force for good in the world since time immemorial. Father Corbishley contended that for the further study of man theology is necessary and he concluded:

True as it is that the tremendous advances which have been made in the physical sciences during the last century, adding immeasurably to man's comfort and his control of nature, have been accompanied by a decline in traditional religious beliefs, it is not less certain that man has never before been faced with such a gigantic threat to his very survival. Science alone points the way to and indeed attains certain limited goals. Theology alone may seem to disregard such objectives in its insistence on one transcendent purpose for man. Yet the two are, in fact, really complementary. A genuine partnership is called for, to give greater immediate content to the categories of the theologians, to ensure that man's greatest values are not sacrificed to the important yet subordinate achievements of science.

To Catholics, and indeed to many other Christians, whatever the nature and destiny of man are concerned, the keynote of all co-operation must be recognition of the unique position of the Church in this respect, and of the Roman Pontiff in particular, wherein is enshrined by teaching and tradition the guardianship of the Faith. Because the Faith and the ultimate destiny of men are of supreme importance, transcending all mundane considerations, the Pope sounded a warning note to all Catholics when he wrote

in the introductory part of *Humanæ Generis*¹ concerning the Faith and the Positive Sciences:

It remains to say something about further difficulties concerned with the positive sciences (as they are called), and yet connected in a more or less degree with the truths of the Christian Faith. Some thinkers are loud in their demand that the Catholic Religion should make these sciences of the greatest possible account. An excellent principle, where it is a question of really ascertained facts; but what of hypotheses, based to some extent on natural science, which yet affect the doctrines in Scripture and in tradition? Here we must be cautious; where such conjectures are directly or indirectly opposed to the truths God has revealed the claim is inadmissible.

The meaning here is clear and salutary. Anything flatly contradicting the known interpretation of revealed truth must be discarded. As Catholics we are well aware here that in the end the contradiction will turn out to be apparent, or it will generally come to be recognized as wrong. Theories and hypotheses in science affecting the Christian Faith are not just to be accepted at their face value. They must prove themselves.

Nevertheless, a question here prompts itself to the scientist, and it is, At what point does a theory enter the realm of ascertained fact? Or, in other words, what is the degree of certainty which must be attained by a scientific theory which touches on the Faith before it can be taken into account by the theologian? To ignore such a theory widely held would seem to be the opposite of co-operation. To judge by precedent, weight of serious opinion will play a large part here. If a large majority of past and present theologians hold to a certain point in theology, it would be temerarious of ordinary Catholics seriously to doubt the point. Likewise, if a large majority of, say, biologists hold to a certain theory, it would also be rash for the biologically uninstructed to doubt it. The instructed person is, in each case, the one best qualified to pass judgment upon the matter so far as the facts embodied in it are concerned.

This topic brings us to the question of evolution and its relation to the Faith. We have seen that the theory of evolution of plants and animals, excluding man for the present, has a tremendous amount of cumulative evidence in its favour; and it

¹ 1950.

is supported on the experimental side by the actual production of new types of organisms. Trained professional geneticists, cytologists, taxonomists and their combinations, cyto-geneticists and cyto-taxonomists, morphologists, anatomists and palaeontologists, who are the scientists most concerned in evolutionary theory, do not seriously doubt that a process of evolution has been in operation in the past, and may even be working at the present. Among these people, who are concerned with these subjects as their life-work and who come to possess a biological 'intuition' as it were, evolution is an accepted and indeed logical and natural phenomenon. This conviction finds great support when it is further considered that no other theory can account for the facts and no other theory susceptible of scientific investigation which agrees with the facts can be imagined. The biologist contends that evolution *is* the only possible explanation of the past and present existence of plants and animals on this earth. In holding to this he is not appealing to mystical forces; he is not philosophizing; but he is merely using the inductive and the hypothetico-deductive methods discussed in Chapter 1 to arrive at a scientific conclusion. In the future the theory may develop, and be superseded by another, but the newer one will not contradict the older, just as the newer knowledge of the structure of the atom does not contradict the older atomic theory—it is a further development of it.

There are doubters, of course, even in the biological world. There are always some people who do not feel constrained to accept theories; they are entitled to withhold their assent providing they are qualified to judge the issue. In the past there have been doubters and critics who have raised every imaginable objection to the theory of evolution, but all of the major criticisms have been given answers satisfactory to biologists (who, after all, should be the judges in biological matters, *sensu stricto*). Any biological criticisms still remaining mostly concern matters of detail.

The theory of evolution, of course, like any human intellectual endeavour, is based on certain assumptions or postulates, but these assumptions have developed over a long period of time and they have become to a large extent axiomatic. Besides, the theory of evolution has been attacked from all sides over the past hundred years and yet it has grown in content, in meaning, in

stature and in certainty, without ceasing over all this period. No fact has so far been discovered in biology which does not fit into the evolutionary scheme sooner or later. It is obvious, of course, that on the large scale no man could observe evolution actually taking place. He cannot sit and watch the fossils being deposited over millions of years, and yet, in their own way, the fossils themselves provide a good substitute for direct observation, unless indeed we accept the stupid contention that all the fossils are artefacts, or put in the earth by the Creator to bamboozle men. When the author was a young, inexperienced student he wrote to Professor J. B. S. Haldane to the effect (as far as he remembers now) that only a recording angel could give direct evidence of evolution. Professor Haldane, who could easily have ignored this impertinence, courteously replied that the fossils were recording angels, or words to that effect. How apt this reply really was!

The biologist then is entitled to ask those non-biologists who deride or deny evolution to produce evidence which should consist of something more concrete than the objections of the few professional biologists they may gather in after diligent search, and then to balance this evidence with that in favour of the theory. The biologist further is entitled to ask also if the non-biologist objector is really aware of the almost unbelievably large amount of literature in existence which is based on some aspect of evolution. So many journals come out every year in nearly every language that it is beyond the reach of any single biologist even to read all the abstracts. The biologist is also entitled to ask if there is any scientific theory in existence which has such a weight of evidence in its favour?

Thus, to the biologist the theory of evolution is well established, and the onus of disproof lies heavily on the shoulders of sceptics. And yet in serious mood, few biologists will assert that evolution is a fact in the absolute sense; they are more likely to ask what you mean by an absolute fact. Indeed few things can be asserted in this sense which will command universal agreement. There is no need to labour this point, all we wish to achieve is to show that, to a biologist, evolution seems to be true enough to warrant the serious attention of others, particularly Catholic philosophers and theologians, in a spirit of co-operation, not grudging acceptance; to warrant too the serious attention of Catholic teachers, writers

and editors of Catholic papers, who are in such favourable positions for influencing those they teach, or their readers. If the only result of such enlightened attention were to be an increase in the number of Catholics professionally interested, who could measure the good that might come of it?

2. *Evolution and 'Humanus Generis'*

The case is rather different when we come to the evolution of man, and we would expect this to be so, if only because of the fact that man is acknowledged to be a unique creature. Man has undeniable animal features. He is therefore, in part, animal, and we would expect him to come under the laws of nature respecting animals. No one would deny these points, but do not let us fall into the 'nothing but' error and imagine that man is nothing but an animal. If animals and plants have evolved, then *a priori* we expect man to have evolved also. That is the expectation, for the biologist sees that evolution is a universal process applying throughout the organic world, and he sees no reason to exclude man as an animal from that process. But, to save possible misunderstanding, let us draw a distinction here. When the evolutionist writes of the evolution of man he may mean the complete man—body and mind (or soul)—or he may mean only his body. On the other hand, when the Catholic (evolutionist or not) and the theologian write about the evolution of man, they mean *only* his body (which includes his brain).

We have already said that the human evolutionist competent to judge does not doubt that man (physical man) has sprung or evolved from the lower creation. From all the evidence available he concludes that man too fits into the general evolutionary scheme; and the evolutionist continually searches for more and more evidence to verify his conclusion. How man has evolved is not so well known and hence a legitimate doubt may remain. Some human evolutionists will say that the evolution of man is certain, and some will say that it is highly probable but has not yet been proved with absolute moral certitude. The evidence for man's evolution is strong enough to justify the evolutionist in demanding another equally reasonable and scientific explanation of the facts so far known if evolution is not accepted.

We may now quote a most important passage from the en-

cyclical of Pope Pius XII¹ called *Humani Generis*. This encyclical is outstanding in that for the first time in history a Pope mentioned evolution directly, nearly a hundred years after the modern theory was first promulgated. Here is an example of wise caution which gives an added importance and significance to the Pope's words.

The Pope wrote, and we quote the passage in full:

Thus, the Teaching of the Church leaves the doctrine of Evolution an open question, as long as it confines its speculations to the development, from other living matter already in existence, of the human body. (That souls are immediately created by God is a view which the Catholic Faith imposes on us.) In the present state of scientific and theological opinion, this question may be legitimately canvassed by research, and by discussion between experts on both sides. At the same time, the reasons for and against either view must be weighed and adjudged with all seriousness, fairness and restraint; and there must be a readiness on all sides to accept the arbitrament of the Church, as being entrusted by Christ with the task of interpreting the Scriptures aright, and the duty of safe-guarding the doctrines of the faith (cf. Allocutus Pone ad membra Academiac Scientiarum, 30 Novembris, 1943; *A.A.S.* vol. XXXIII, p. 506). There are some who take rash advantage of this liberty of debate, by treating the subject as if the whole matter were closed—as if the discoveries hitherto made, and the arguments based on them, were sufficiently certain to prove, beyond doubt, the development of the human body from other living matter already in existence. They forget, too, that there are certain references to the subject in the sources of divine revelation, which call for the greatest caution and prudence in discussing it.

There are several points about this most welcome statement by the Holy Father which we may consider in a little detail below. There is no question whatsoever of the evolution of the human soul. Each human soul is created individually by God, presumably at conception, that is, at fertilization, or near to it, although there are different opinions about the time when it occurs.² It has always been clear to Catholic theologians that the soul as the form of the body could not evolve, or be the product of an evolutionary process, that is, it could not change its nature. This fact is seen immediately when we consider that for a human soul to evolve in

¹ 1950, para. 36.

² See animation theories in *Messengel*, 1954.

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the strict sense would mean it would have to change into an angel or some other higher spirit. Each human soul is truly unique, that is, it is a creation '*ex nihilo*', and being immortal, it cannot change into another for it would then lose its identity. The Church has always taught the uniqueness of the human soul and its personal individuality which is part of Revelation and hence absolutely true. No amount of scientific or other knowledge can affect this truth and to disbelieve it, or worse to ignore it, ultimately leads to the degradation of man—a process we are unfortunately witnessing in this century. Hence, those evolutionists who contend that the mind of man is merely a development from the animal mind are clearly wrong. No Catholic can subscribe to this idea without falling into grave error.

It is not a necessary unavoidable conclusion to draw, either from comparative anatomy, morphology and physiology, or from evolutionary evidence, that the mind of man is only a highly developed animal mind, or that it evolved from an animal mind. There is no evolutionary evidence of the gradual transition of an animal mind into a human mind, and no serious biologist would contend that there is. Although a great deal is known about the structure of the brain through which the soul works, and the normal and pathological status of many men has been studied, in effect there is still a very great deal about the human mind which we do not know; only the fringes have been explored. The relation between mind and matter has been a live issue for many years and will be for many more to come. Philosophy and philosophical psychology would seem to give more information about the soul than positive science because they can get down to a consideration of the soul's essence which science is unable to do. To prove that man's mind or soul has evolved it would be necessary to prove that this human immaterial soul is not different in kind from the sentient material mind of an animal. As this involves a contradiction, it could only be attempted either by proving that the mind is not distinct from the brain and thus solving the problem of mind and matter (a *denial* of the distinction, or of the existence of a problem, is not proof), or by denying and disproving the existence of what the theologian calls spirituality and intellectuality in man. Only a materialist would attempt to do this because a non-materialist realizes the futility of it.

Hence, it follows that no Catholic can hold any materialist

views of evolution. Incidentally we may note that it has been the propagation of this kind of materialistic evolution which attempts to make man nothing but a completely material animal body who has sprung completely from an animal level, which has helped to continue the antagonism between the theologian and the evolutionist, and to make the theologian doubtful of the value of a theory which teaches such grave error.

Inasmuch as Catholic philosophers teach that the soul infuses, or informs, the whole of the body, we cannot say that it is in one part more than in another. Hence, it is incorrect to say that the soul 'resides' in the brain and nowhere else.¹ The brain is the material vehicle through which the soul acts intelligently during life. Thus although it is *de fide* that the soul of man is individually created, one can hold that the human brain has evolved from a lower animal. The human fossil evidence is largely bound up with the evolution of human skulls and, by implication, the human brain. The materialist evolutionist would here consider that if he shows the human brain has evolved then *ipso facto* the mind or soul has evolved too. But this is a position forced on him by his initial postulate that only matter exists. If he acknowledges an immaterial element in man he is forced to consider that this too has evolved from material matter, and this is a plain contradiction. Catholic philosophers prove the existence of immateriality. And the contradiction inherent in the evolutionary materialist assertion lies in the fact that a material body has parts, is extended; while an immaterial thing is simple, is unextended. It is impossible for a simple thing to be formed from an extended thing. To say that the immaterial can evolve from the material has no positive intelligible content; it is meaningless.

The Pope acknowledged the possibility of the evolution of physical man from some lower animal. This is not to say that in the mind of the Church the matter is certain or probable, but it is a statement of the fact that to hold such a view is not contrary to Scripture as so far interpreted by the Church. The matter is at present an open one, and the pros and cons may be seriously discussed. A condition of its legitimate discussion is that the question should be considered with respect and no antagonism on both sides. This would not prevent both sides from criticizing the findings and opinions of each other. The statement is clearly

¹ The soul does not reside in the body at all—it is that which makes the body a man.

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meant to give importance to both scientific and theological findings on this question. This serious discussion should be between experts, that is, those who, by training and qualification, are competent to understand the implications of their researches. Unwarranted assertions by inexpert people of both sides can then be ignored, and the opinion of such should not enter into serious discussions. By implication, the points at issue may be taught by those who, while not having the highest competence in the matter, are yet sufficiently qualified to expound it. The Pope mentions experts on both sides, and this can scarcely mean that those who discuss human evolution must be expert biologists (or anthropologists) *and* expert theologians. There are very few of the highest biological authorities on human evolution who would claim much qualification in theology. With understanding and sympathy on both sides an expert theologian should be quite able to discuss the matter with an expert evolutionist and *sic et vice versa*. In view of the position and authority of the Church which is God-given, and the special nature of man, the Pope expects all to submit the matter finally to the Church. All Catholics unhesitatingly agree to such a course.

We can note also that there have been Catholics who were rebuked by the Pope for taking the evolution of man for granted, as though it were completely certain. As already pointed out, the evolution of man follows from the general theory of evolution as an *a priori* possibility, but the state of the fossil evidence while strongly indicative to biologists must yet contain an element of doubt in it to the theologian. It is not absolutely certain that man has evolved in the way envisaged by evolutionists. There have been biologists who have maintained that the human stock stretches far back into geological time, as far back as the time of emergence of the mammals. The discovery of Tertiary man would upset many of the theories which have been proposed. Finally, the Pope pointed out that Revelation is concerned in the matter.

It is important to note that in this passage the Pope was concerned only with the subject of human evolution. Research and discussion on the subject are allowed which implies it is not contrary to Faith. If this is so, then by implication, evolution in general is also a legitimate subject for Catholics, because in a biological sense the evolution of man is only a part of the larger

idea of evolution which includes all animals and plants. Without an evolutionary scheme of plants and animals it would scarcely be possible to formulate a scheme of human evolution. We may then assume that there is nothing in the idea of the evolution of plants and animals and man derogatory or contrary to Faith, subject always to the operation of the Divine Concursus.

In an earlier passage of *Humani Generis*,¹ however, the Pope in a discussion of present-day fallacies wrote:

Some will contend that the theory of evolution, as it is called—a theory which has not yet been proved beyond contradiction even in the sphere of natural science—applies to the origin of all things whatsoever. Accepting it without caution, without reservation, they boldly give rein to monistic or pantheistic speculations which represent the whole universe as left at the mercy of a continual process of evolution. . . . These false evolutionary notions, with their denial of all that is absolute, fixed or abiding in human experience have paved the way for a new philosophy of error. Idealism, immaneism, pragmatism, have now a rival in what is called 'existentialism'. Its method, as the name implies, is to leave the unchanging essences of things out of sight, and concentrate all its attention on particular existences.

It would seem that here the Pope was commenting on a general cosmic theory of evolution rather than on human evolution alone. It would appear that he did not mean organic evolution or even the evolution of animate from inanimate matter, otherwise there would have been no need for the later comment on human evolution in the same encyclical. This passage was surely a condemnation, not of the scientific theory of organic evolution as such, but of the various and erroneous implications which have been placed on it by various writers. The remark about 'the mercy of a continual process of evolution' surely does not mean that evolution must have been discontinuous but that it is wrong to picture it as being controlled by 'blind chance', which many of the earlier Darwinians advocated and which again probably led to much antagonism with theologians. It is clear to Catholics that in whatever way evolution does work, it does so only through the operation of secondary causes and, however much it may appear to be undirected when viewed from the angle of its secondary causes, such as selection, the First Cause is necessary for its

¹ 1950, paras. 5-6.

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initial beginning and the Divine Concursus is necessary to maintain it in operation.

In our discussions in earlier chapters we have mentioned that in spite of what seems to be the haphazard method by which selection works on organisms, a view of the process *in toto* unmistakably shows the operation of law, and that evolution works towards an end, and we may say that that end is man. Some evolutionists unfortunately oppose finalist theories in evolution. For example, G. G. Simpson¹ had much to say about it. He opposed what he called *finalism* which he practically equated with vitalism of the Driesch type and which is rather a scientific theory than a philosophical one, but he argued as though he meant *finality*, which is a philosophical concept. As far as we understand him, he seemed to think that finalism, in the sense of finality, contradicts, or stands in opposition to, causalism (by which he meant causality). These opinions led him to hold that man is just the 'result of a purposeless and materialistic process that did not have him in mind. He was not planned'. Simpson maintained that evolution is purposeless and has been so from the beginning. It would seem that, according to Simpson, teleology is just non-existent. This is the kind of conclusion drawn from materialistic evolutionary ideas which the Pope condemned and which no Catholic would agree with.

Scientifically and philosophically, materialism is in a weak position, and as regards finality and teleology we may quote W. R. Thompson.² He wrote:

If it were possible to construct a theory of Evolution representing this process as due to pure chance, antifinalists might have some cause for satisfaction and finalists some cause for alarm. It will, however, be evident from what has already been said that a Universe of pure chance is, in the strict sense of the word, unthinkable, by which we mean, not simply something distasteful or dissatisfying, but something on which the mind cannot take hold at all. A world of pure chance is simply chaos, or *absolute disorder*, and the concept of absolute disorder has no positive intelligible content. Chance or fortuity is a by-product of finality. The fact that a certain event, or collection of events, is due to chance, therefore, does not annihilate the doctrine that finality exists in the Universe; without the assumption of finality the proposition could not even be stated.

¹ 1949, and p. 342. ² 1937, p. 218.

Evolution may seem to some minds to be fortuitous but this is because we do not know enough about the process, about its causes and their interactions to predict the result. When we consider the complexity of the process it may seem that we may never be able to give a complete analysis of it. To this extent the view which we have of evolution is always partial, and much is hidden from us, especially the end-view of evolution. As far as natural selection is concerned de Beer¹ also pointed out that this factor of evolution 'cannot be regarded as the result of chance'.

A famous biologist, H. J. Muller,² said: "'Purpose' is not imported into nature, and need not be puzzled over as a strange or divine something else that gets inside to make life go: it is no more an added force than mind is something in addition to brain. It is simply implicit in the fact of organization, and it is to be studied rather than admitted or 'explained'." Basic concepts like purpose, etc., have long been a bogey to many biologists; their rejection leads to pure materialistic interpretations of evolution, like that of G. G. Simpson above. But these concepts, while they may have been excluded from biology by some biologists, have never in fact been absent from it. We see that their attempted exclusion gives only one facet of a picture which in nature has no equivalent reality, and thus must lead to distortion and error in the resultant interpretation.

An excellent concise account of some modern views of purpose and ends in biology has been given by Bernard Towers,³ and to give some idea of the place of teleology in biology we give a short summary of his views below. It is clear from biological literature in general that the word teleology has been given several meanings. Towers analyses them according to the diagram in Figure 27.

Clearly when we talk about ends and purposes we have two concepts in mind: (a) an end in view, which is the purpose strictly speaking and (b) the end result. In Thomist terms category 5 in the diagram means that all the efficient causes concerned produce a result which is inherent in the physical set-up. It can be reproduced and represents order not chaos. The exposition of this concept was due to Aristotle and the Schoolmen, and it was one of the factors contributing to the advance of modern science.

¹ 1938, p. 16, and see pp. 263-264. ² 1943, p. 169.

³ 1937, pp. 355-364 and 408-417.

Towers said that extrinsic finality implies purpose introduced into the universe from without; while intrinsic finality is the purpose which is peculiar to biological systems. Category 1 corresponds to the 'Design' of Paley, while categories 3 and 4 are at the back of all the 'emergent' and 'creative' evolution theories. Category 2, as Towers wrote, 'implies that there *is* some overall divine end-in-view or purpose in the universe, but that the purpose works in and through the operation of scientific law (except in so far as miracles are concerned). It seems to me that Henderson and possibly D'Arcy Thompson argue in an inductive way towards this conclusion, and I find their accounts intellectually compelling.'

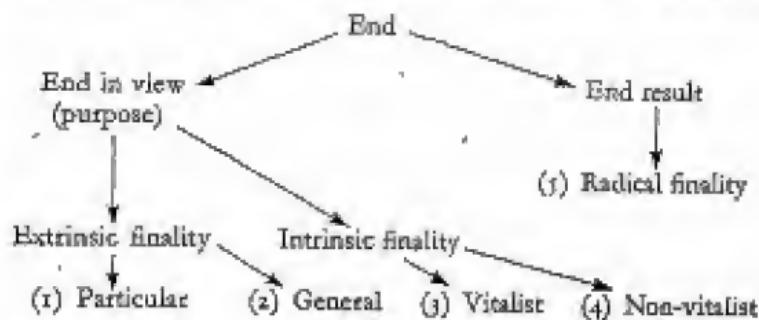


Fig. 27. Diagram giving an analysis of teleology and finality. (After Towers 1937, see text.)

But this category of meaning of teleology could be arrived at logically, I think, from analysis of the implications of category 3'.

Many Catholics would endorse Towers' views in this regard, and they seem to be the traditional views of the Thomists at least. In the course of time it seems that the concept of teleology became enlarged to indicate features not inherent in the minds of the original thinkers who discussed the concept. Many of these later meanings have not stood the test of time as with the vitalist ideas. But with the retreat of the vitalists, the impression arose that finality and purpose in all their meanings were being discarded and discredited. As far as evolution is concerned the result was a materialistic interpretation based on false premisses.

3. Evolution and Catholic Sources

In the passage from *Humani Generis* quoted earlier the Pope almost casually mentions that there are references to the origin of

man in Scripture which must not be ignored. The biological and anthropological study of the origin of man can only be studied by the methods of biology and anthropology which have their limitations. But Revelation is certain and its meaning when discovered, or interpreted authoritatively, is absolute. Scripture then should be a guide to the scientific study of man's origin. As things are, few of the authorities who study the evolution of man are also experts on Scripture, and hence it is that theologians have been almost wholly responsible for the study of that aspect of the subject. In practice this study has largely consisted of arguments as to the meaning of Scriptural passages regarding the origin of man between those who upheld the biological theory, those who kept an open mind about it, and those who were opposed to it. Besides the study of the Scriptures themselves, the interpretation and teachings of the Fathers of the Church, and the teachings of Tradition, were also involved.

The study of Church sources of this kind is highly specialized. Hence the interpretation of evolution in the light of Faith is a complex task and often turns on the meanings of words and phrases in the Scriptures or the commentaries of various acknowledged authorities. It is true that at first sight some evolutionary ideas did seem to stand in opposition to the teachings in the Bible, and this fact in itself increased the difficulty of reconciling the two. Fortunately the position today is much easier and better understood, due in no small measure to the erudite and classical works of the late Mgr. E. C. Messenger and the late Canon H. de Dorlodot.¹

By giving an account of Messenger's conclusions the historical approach which we have adopted in much of this book will be maintained. In *Evolution and Theology* Messenger first examined the idea of spontaneous generation, that is, of the production of animate from inanimate matter. This is a subject which does not concern us here; the organic evolutionist at present starts with life and works from that point onwards. Ideas of the origin of life ultimately affect our view of evolution but that stage has not yet

¹ See E. C. Messenger, 1931, 1949, 1954; H. de Dorlodot, 1915. I would like to acknowledge my indebtedness and my appreciation of the works of Messenger and Dorlodot. Their books must be a fruitful source of information not available otherwise to those who are not theologians.

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been reached in evolutionary studies.¹ Nevertheless, we may say that spontaneous generation was an accepted view from very early times. In an earlier chapter we saw how many of the ancient philosophers pictured living things arising from the primary elements, often in a fixed order. It was only in the last century that Pasteur and Tyndall showed that there was no evidence to support abiogenesis, as spontaneous generation is called. They did not, however, disprove its possibility and the topic is seriously discussed at the present time. From the theological viewpoint Messenger showed that Scripture implies in general that the origin of living things was due to secondary causes, that is, due to powers put in inorganic matter by the Creator. Up to the time of the 13th century apparently the Fathers of the Church and theologians interpreted Scripture in this way regarding spontaneous generation. The scholastics in the 13th century, however, broke away from this view. This attitude was no doubt due to their faulty ideas of physics. We must not think that all theologians agree with Messenger's views in this regard.²

In science, opinion about the matter has also ebbed and flowed but in modern times it seems that, with more understanding of the constitution of the viruses and with advances in protein and enzyme chemistry, opinion is again beginning to accept the possibility of its occurrence. The important point seems to be that if science ever proved the occurrence of abiogenesis and the Church ever accepted it as true, there would be no serious difficulty with regard to the Scriptures and the teachings of the Fathers.

We come now to organic evolution in general. Messenger³ wrote:

As to the *evolution of species*, we consider that the *scientific* evidence, consisting as it does of so many converging lines, is sufficient to give a fairly high degree of certitude concerning the *fact* of, at any rate, *some* evolution, though opinions must necessarily differ as to the *mode*. And from the *theological* point of view, we consider that evolution is the only reasonable way of harmonizing our modern knowledge of the succession of geological epochs, with their flora

¹ Theories of the origin of life are all speculative, and for a short modern account the reader may consult P. G. Fothergill, 1938, which also contains full references.

² See Messenger, 1949.

³ 1931, p. 274.

and fauna, with the Scriptural statement that the earth produced all the present-day species.

This is a cautious statement. Without absolute evidence a theologian could scarcely say anything stronger than 'a fairly high degree of certitude' concerning a scientific matter. So far there has not been any official condemnation of Fr. Messenger's views in this regard, and indeed, as we have seen, *Humani Generis* of 1950 gave support by allowing the scientific discussion of man's evolution. A biologist, in Fr. Messenger's place, would probably prefer stronger language regarding the evidence and this could be achieved by omitting the word 'fairly' in the phrase 'a fairly high degree of certitude'. Further, since Messenger originally wrote it, a new approach to the *mode* of evolution has appeared and has gained ground rapidly among evolutionists. In spite of the complexity and detail of the evolutionary process modern biologists would probably say that we have sound knowledge of the mode of evolution.

When we turn to the Fathers of the Church and theologians, Messenger points out that it is impossible to deal with every comment by every writer on the origin of living things, and hence he selects for comment those who belong to the literal school of interpretation of Genesis. Another reason for this choice is that the Church has told us that the *literal historic sense* of Genesis must be accepted. It is important to note the distinction between the literal historic sense and the purely literal sense. The latter means the sense of the words as we see them today, that is, their literal obvious meaning in these times. The literal historic sense is more difficult to attain. It means the literal sense of the words in so far as we know them but in the historic context in which they were written, and to ascertain this meaning recourse must be made to many sources of ancient history to discover the literal meaning of the words to the people to whom they were addressed.

The Fathers and other writers mentioned by Messenger are given below. St. Ephrem in the 4th century taught that plants and animals were produced by the active power of the elements. St. Basil in the same century held that the earth produced the plants and the same applied to the animals. St. Gregory of Nyssa considered that, like the Alexandrian School, all things were created potentially at once by the Creator, and their subsequent

appearance was brought about by the development of the potencies first created 'according to a fixed and necessary order of succession'. Messenger remarks: 'This profound doctrine of the virtual creation of all things at the beginning of time is, we consider, one of the greatest achievements of the Patristic period, if not of the whole of the Christian era.' The creation of things *in potentia* allows for their subsequent evolution. St. John Chrysostom also taught that, according to Scripture, plants and animals were first produced by the operation of earth and waters as secondary causes at God's command. We may remark that there are certain similarities between these views of Scripture and those of some of the early pagan philosophers. In the case of the latter their views have been considered as showing glimmerings of an evolution idea.

The teachings of St. Augustine, Bishop of Hippo, recall those of St. Gregory of Nyssa, but there are important differences. St. Augustine considered that there was an actual creation of inorganic things, but only a potential creation in the case of living things. And so we may progress through the works of the Venerable Bede, St. John Damascene, St. Bonaventure, up to but excluding St. Thomas Aquinas, where similar views are given. Hence Canon Dorlodot¹ could write:

Some authors explicitly profess the theory of absolute natural evolution of living things in the sense of St. Gregory of Nyssa and St. Augustine. Others repeat more or less in their entirety the assertions of St. Basil; lastly, there are some who remain silent on the matter, and limit themselves to expounding the order of appearance of the different creatures, and the meaning of the six days of the *Hexaemeron*. But we have not been able to find a single Christian writer previous to the Scholastic period who opposed the theory, or who endeavours to regard the *rationes seminales* of St. Augustine simply as material or passive powers, as later writers endeavoured to do.

St. Thomas, however, on the basis of Aristotle's physics, took a different view from his predecessors. He taught (a) that the terrestrial bodies took an active part in the production of plants and inferior animals; (b) that the higher animals were produced directly by God. And so as we proceed through the centuries we find some theologians agreeing with the early Fathers and others

¹ 1923, p. 64.

agreeing with St. Thomas. It is clear there was no fixed view about the matter. Hence Father Messenger¹ could conclude as follows: 'All things considered, we think we are entitled to conclude from the foregoing citations that *evolution as a hypothesis* applied to the origin of plants and animals has won its *Droits de cité*, and there is no reason whatever to prevent a Catholic from adopting it if he wishes to do so. And further, if science could prove the reality of spontaneous generation, a Catholic should welcome this, for it would enable him to give complete assent to the teaching of the Fathers on the point.'

In his book *Theology and Evolution*, Messenger printed some of the reviews of his first book *Evolution and Theology* with his comments and subsequent discussions between the reviewers and himself. The reviewers were all priests as follows: Dr. Rhodes, Dr. Meagher, Dom C. Butler, Dr. Flood, Canon Morgan, Dr. Michael Browne (Bishop of Galway), W. McClellan, Dr. W. J. McGarry, B. F. Sutcliffe, A. Janssens, Dr. Bittremieux, A. Brisbois, J. Gross, Père Lagrange. The book also included comments by Messenger on Fr. Boyer's *De Deo Creante*, a final chapter by Messenger; and the second part of the book was devoted to a study of animation theories by Messenger, Canon Dorlodot and Bishop Browne. To a certain extent then this valuable book summed up modern theological opinion regarding evolutionary ideas and the Scriptures.

Some of the views expressed agreed with Messenger's conclusions regarding evolution and the Fathers; some opposed him almost completely; and some disagreed with parts of his original thesis. It is clear that opinion regarding both spontaneous generation and the development of living things is very much in the air as far as theologians are concerned. Beyond the basic teaching of the Church which we have already from Pope Pius XII, there is no unanimity of opinion regarding the details of these matters. We are unable to give the views of the various authors listed above—for this another book would be necessary. In a sense the conclusions of the Rev. Dr. Meagher² summed up many of the views expressed as follows: 'Now for the inevitable questions: Is the Bible favourable to evolution? My answer to that is in the negative. Is it opposed to evolution? Again I answer negatively. Are the Fathers favourably disposed to evolution?

¹ 1931, p. 84.

² In Messenger, 1949, p. 18.

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No. Are they then opposed to it? No, I do not think so, because they never thought of it.'

4. *Evolution and the Creation of Adam and Eve*

Certain documents of the Church should now be mentioned to complete the account we have already given. Documents of this kind, while they are authoritative in their meaning, are not meant to be infallible pronouncements. They should be approached in the historical spirit of the times in which, and bearing in mind the purpose for which, they were written and the circumstances which called them forth.

In 1909 the Pontifical Biblical Commission established by Pope Leo XIII in 1902 issued a Decree, which had the assent of the Pope, and which contained answers to eight questions. All of these questions were concerned with the historical character of the first three chapters of Genesis. This Decree laid down that the literal historical sense of Genesis must not be doubted and by this is meant the literal sense in which the people of the times when Genesis was given would have understood it, and Genesis is not here teaching science or history in the ordinary way. Among others, the Decree also gave what the Commission called four fundamental truths which are intimately connected with the Christian religion. These were:¹

1. The creation of all things by God at the beginning of time.
2. The special creation of man.
3. The formation of the first woman from the first man.
4. The unity of the human race.

Concerning these matters the sense as given in Genesis is not metaphorical or anthropomorphic, but literal in the historical sense; although the chapters may contain metaphorical and anthropological elements.

Then, in 1941, Pope Pius XII gave an address to the Pontifical Academy of Science which further emphasized these Decrees by stating:

1. The essential superiority of man in relation to other animals by reason of his spiritual soul;

¹ See *Messenger*, 1949, p. 187.

2. the derivation of the body of the first woman from the first man, and
3. the impossibility that the father and progenitor of a man could be other than a human being, i.e., the impossibility that the first man could have been the son of an animal generated by the latter in the proper sense.¹

Later, in 1948, a letter was issued by the Secretary of the Biblical Commission to Cardinal Suhard, Archbishop of Paris, in which was upheld the essential spirit of the 1909 Decrees, including the importance of the literal historical sense in interpretation, but which allowed discussion in the light of later discoveries.² Next, *Humani Generis*, already mentioned, was issued in 1950. In this document it is declared that the study of the evolution of man's body may be pursued by those concerned under certain conditions. And then the Pope wrote:³

There are other conjectures, about polygenism (as it is called), which leave the faithful no such freedom of choice. Christians cannot lend their support to a theory which involves the existence, after Adam's time, of some earthly race of men, truly so called, who were not descended ultimately from him, or also supposes that Adam was the name given to some group of our primordial ancestors. It does not appear how such views can be reconciled with the doctrine of original sin, as this is guaranteed to us by Scripture and Tradition, and proposed to us by the Church. Original sin is the result of a sin committed, in actual historical fact, by an individual man named Adam,⁴ and it is a quality native to all of us, only because it has been handed down by descent from him (cf. Rom. 5: 12-19; Conc. Trid. sess. V, can. 1-4).

The position of a Catholic regarding the evolution of man is quite clear, but there may be some difference of opinion regarding his mode of evolution. Some theologians contend that Adam was specially created *in toto*, others that secondary causes have played a part. If we accept the evolution of man from the lower creation a difficulty arises in connection with the problem of how an animal father and mother could produce a son (see the third point given by the Pope mentioned above). The Pope said that Adam could

¹ *Messenger*, 1949, p. 182.

² Suhard, Cardinal, see *Acta Apostolicae Sedis*, 1948, and *Clergy Review*, 20, pp. 423-425, June, 1948.

³ 1950, para. 37.

⁴ The translation used here is that of Mgr. R. Knox. This phrase means only that Adam was an actual living person.

not have been generated from an animal father in the *proper sense*, and this is a sense which goes beyond the biological facts of reproduction. Thus, the answer to this problem may only be given by philosophy bearing in mind the biological facts of reproduction in which a male sperm unites with a female ovum. On the evolutionary theory these sex cells, in the case of Adam, may only have been produced by prehominids, i.e., from animals. If this were so then these sex cells could have been the *instrumental cause* of the production of Adam inasmuch as they furnished *in potentia* the biological requirements of the human body. In the ordinary way the body they produced would have lacked a human soul and so the resultant creature would have been purely animal. But if these cells acted by the *situs* of God to 'receive' a human soul when the requirements for the formation of a body fit to be human had been biologically fulfilled, then, in a sense, God would be the actual 'father' of Adam. In ordinary human reproduction the soul infuses the body some time between actual conception and birth. According to those who advocate mediate animation as opposed to immediate animation the soul only infuses the body when the latter is fit to receive it, by which is meant the stage when the embryo undeniably possesses the mental and nervous mechanism enabling it to be distinctly human. The first created human soul may have been infused in a manner analogous to this method.

If this philosophical explanation is correct then it is legitimate to pursue the matter along biological lines. If the Pope's words were to be taken literally then it would mean that Adam could have had no genetic connection whatsoever with the animal world and at the same time his evolution from the lower creation may be studied and investigated, and hence we could only look for his production either by a direct creative act of God or from a man and woman already in existence. A modern review of opinions regarding the evolution of Adam and Eve has been given by J. O'Neill¹ in two excellent articles which support the metaphorical interpretation of parts of Genesis as given later in this section, while for a good general modern account of Genesis the reader may be referred to Margaret T. Monte's *Thinking about Genesis* (1953). We will return to this topic shortly.

The Decrees of the Biblical Commission and the Papal state-

¹ 1959.

ments indicate that the present human race is descended from Adam alone, who was a single human individual, and the word 'present' is a keyword in the context used here. Some people have held that Adam was rather a group of individuals who sinned collectively, but the Pope pointed out that such a view cannot be reconciled with the doctrine of original sin, and such a view would also seem to oppose the concept of the unity of the human race. As the *present* human race are all descended from Adam, evolutionary ideas, such as the existence of distinct types of human being, may be valid if they were not actually and ultimately descended from Adam, provided all of them perished at, or before, Adam's time, or left no descendants after him. Human palaeontology indicates that some at least of the ancient types of early man were geographically fairly widespread; *Pithecanthropus*, for example, lived in Java, China and possibly Africa. Pre-Adamites, if they ever existed, might also have been widely scattered. It is difficult to visualize how they could all perish by natural means in a relatively short time. We have already noted that one famous systematist, E. Mayr,¹ has proposed to classify the recent hominids into one genus with three species as *Homo transvaalensis*, *H. erectus* and *H. sapiens*. The first of these is doubtful but the second is human or near human. Further, Mayr considered that there is no evidence to show that more than one species of *Homo* was in existence at any one time. Hence, if this is true, *Homo (Pithecanthropus) erectus* may have been a Pre-Adamite—that is, a race of full human beings from which Adam might have sprung when this race was in its last stages of existence. If, however, the human races, or kinds, found so far were really different and if they, or some of them, were co-existent with each other, then it is difficult to visualize how they could all perish, except one race, by natural means in a relatively short time.

On the other hand, perhaps it would be better to consider Adam as the absolutely first human being of all. There is no serious evolutionary reason why all men should not have descended from a single original pair, and this indeed is what biologists would expect. The development of even two, let alone a large number, of original men of independent origin would indeed be a unique example of an extraordinary number of cases of convergence or parallel evolution which would be the more astounding when we

¹ 1950, pp. 109-118.

consider the vast chasm between man and the lower creation.¹ But this argument does not exclude the possibility of the existence of Pre-Adamites who may not have been truly human except nearly so in a physical sense. The Church has not yet given any decision about the existence of Pre-Adamites, except that they must have ceased to exist after Adam's time if they were truly human, but their extinction would not be necessary if they were prehomomimids.

It is possible that part of the difficulty in conceiving the evolution of man lies in the fact that we all tend to regard Adam as having been a man just as we are at present. Possibly we look upon him as having been a kind of Adonis. But if we can get rid of such preconceived ideas it is easy to see that in all probability the first man was very brutish in appearance, and certainly not Adonis-like by our present-day standards of beauty. After all, why should Adam have had the appearance of a modern European? It is reasonable to suppose that man's body has undergone small changes affecting his appearance since Adam was created and indeed it has done so in the production of the various white, yellow, and black races. Consideration of the probable appearance of the various types of men revealed by the human fossils indicates quite clearly that early men were animal-like in their appearance. This is shown by such features as the prognathous jaws and the prominent eyebrow ridges, to mention only two features.

Granted the points we have mentioned, then it is possible to speculate further on the formation of Adam. Biologically, in the present state of our knowledge, the only way in which Adam could be produced is through the agency of sexual reproduction involving the fusion of two gametes, that is, it implies the prior existence of male and female parents. It is really inconceivable to see how a human being or higher animal could be formed in any other way.² If these gametes could act as instrumental causes then Adam could have arisen from prehomomimids or non-spiritual Pre-Adamites.

¹ See also pp. 200, 291-292, and footnote 2, p. 230.

² This statement does not exclude parthenogenetic development of the egg, but it does exclude the parthenogenetic development of the male gamete alone. If an egg developed without fertilisation it could only produce a female because it would lack the Y chromosome. But there are no authentic cases of human parthenogenesis on record, excluding the Virgin Birth. The embryo can only be nurtured in a female body and hence a male gamete is excluded from parthenogenetic development by this fact alone, except in very special, but imaginable, circumstances.

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Let us try to picture the situation in modern terms as it may have been at the time when Adam was created. The fossil evidence indicates that scattered about the world there were small populations of various kinds of man-like creatures. Some may have been more man-like than others. Perhaps in one of these populations mutations began to arise which gradually pushed the physical appearance of these creatures away from the animal type towards the man-like type and which set the further development of the brain in motion. If such mutations were recessive and small, according to modern population genetics they would be present as heterozygotes for a very long time quite unrecognized, but gradually they would accumulate and become dominant, ousting the previous more animal-like dominant type. For similar mutations and a similar process of emergence to arise in other populations would be biologically very unlikely, if not impossible, because of different conditions and environment in other populations and situations. Hence these prehominids would be concentrated in one local, perhaps relatively small, geographical area, or even ecological niche.

Once the specifically human physical characteristics had become dominant the evolution of the population could have progressed very quickly until creatures very near to man had arisen. Among this population at this stage some individuals would be in advance of their fellows, some whose gait was practically erect, who had started to lose hair, etc., and whose brain may have been fairly large and advanced in structure. Perhaps at the conception of one of these more advanced types the genetically near-human gametes became the instrumental causes in the formation of the first human being which at the moment of conception received a human spiritual soul. And these gametes could have carried the final mutations making the full physical development of a man possible when fusion between them occurred.

Adam would then have been born among a population of individuals many of whom, perhaps most of whom, would have been very like him physically. Some theologians have been repelled at such ideas because they have seen great difficulties in the upbringing of a human child by animal-like creatures. Granted it would be difficult to imagine a modern European baby in the midst of apes. But is it so difficult to imagine a baby in the midst of a *Pithecanthropus* population? We may note here that some

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human palaeontologists consider that *Pithecanthropus* was near-human, that is, prehominid, even though he may have used fire. In such a population the baby could be nurtured and grow up long before he could realize in the normal course of human development that he was somehow different. The intelligence and feelings of a child develop only slowly. As the child grew up he would gradually realize there was some difference between him and his companions; but his occupations, likes and dislikes would have been similar to those of his companions. His spiritual soul would give him higher feelings and insight which would have enabled him to 'walk with God' during all this process of development, until he realized he was 'alone' and needed a companion. He would have been like a genius in the midst of a very mediocre family, and are such cases unknown at the present time?

Another of the real difficulties raised by the theory of the evolution of man is to account for the formation of Eve. This difficulty is so great as to prevent many theologians accepting the physical evolution of man in spite of the biological evidence. Part of the difficulty is due to the fact that early writers accepted the literal story that Eve was formed from the rib of Adam. However, this is not necessarily true; many other authors did see that it could be in some way metaphorical; Cajetan, for instance, in the 16th century, held such a view. Thus the miraculous origin of Eve from a rib of Adam is not a *de fide* doctrine. The Biblical Commission phrased its opinion very cautiously: *formatio primae mulieris ex primo bosque*: the first woman was formed from the first man. It thus tacitly accepted that the story of the rib was metaphorical, and left the field open for discussion of the exact force of the metaphor.

What is the metaphor? Many suggestions have been made, some along very fanciful and not biologically sound lines. For instance, it has been suggested that Eve arose from one of Adam's chromosomes. But one human chromosome does not contain the potentialities of a human being: all the missing chromosomes would have to be created *ex nihilo*. Again it has been suggested that Eve developed from one cell of Adam. Biologically it is possible for a gamete or sex cell to develop into an adult individual. Parthenogenesis is not uncommon in some plants and animals, and there are several other forms of asexual reproduction and of reproduction from haploid cells which later undergo a division to

ensure that the normal number of chromosomes is formed. None of these examples, which indeed are normal to the organisms possessing them, have been seen in human beings, or even in the higher animals. It is possible, of course, that the biological conditions at the time of Adam were very different from those we know at the present time, but, in any case, such parthenogenesis could only occur in the human female not in the male. Male parthenogenesis in the way envisaged is thus biologically unsound.¹

E. C. Messenger favoured a method involving parthenogenesis, but he freely admitted it was only a speculation, as all these ideas must be. Physically a man, so long as he remains a male, is quite unable to produce another human being, male or female, directly and unaided. In the present state of our knowledge biology does not give any indication of how Eve may have been formed other than through some method involving the process of sexual reproduction. Moreover, if Eve was formed from Adam's body directly, excluding any sexual reproductive method, then another biological difficulty arises which does not seem to have been considered up to the present. We refer here to the sex chromosomes. In human beings the sex mechanism is genetically controlled by the *X* and *Y* chromosomes. The male possesses one *X* and one *Y* chromosome. These are homologous but are identical in only a relatively small region of their lengths; otherwise they are different. The female possesses two *X* chromosomes which are homologous and identical. In the inheritance of sex these chromosomes move very precisely so that offspring (excluding accidents) are always *XX* (or females) and *XY* (or males). If a female were to be produced from a male an *X* chromosome would have to be added somehow and a *Y* chromosome lost. Such a change would be different biologically from cases of men alleged to have become women in later life.

However, there is yet another approach to the text of Genesis which would take the story of Eve's creation as metaphorical but as a metaphor which has nothing to do with her physical origin. To appreciate such views properly it is necessary to rid our minds of many preconceived ideas about these parts of Genesis. The author of Genesis is not primarily interested in the physical facts of man's creation, but in the deeper, religious truths of man's

¹ See footnote p. 311.

relationship to God, of the dependence of man on God and of the loss of supernatural grace. As far as the physical truths are concerned, the writer, or writers, of Genesis were not present at the formation of Adam and Eve, and all that could normally be expected is that they should express the Divine truths in the light of the knowledge and ideas of the times.

In Genesis, Chapter 3, verse 20, we read: 'And Adam called the name of his wife Eve: because she was the mother of all the living.' In the original language used Eve's name was *Hawwah* which is connected to the Hebrew verb *hayah* meaning 'to be'. *Hawwah* is not a proper name, but rather describes Eve as the mother of the human race in the same way that Adam simply means 'man' and is likewise connected to the word *adamah* meaning 'earth'. The creation of man and woman is given in Genesis, Chapter 1, verse 27, as 'And God created man to his own image: to the image of God he created him. Male and female he created them.' There would seem to be no suggestion here that man was created first and woman later. But Genesis, Chapter 2, verses 18-24, gives a fuller account as follows: 'And the Lord God said: It is not good for man to be alone: let us make him a help like unto himself. 19. And the Lord God having formed out of the ground all the beasts of the earth, and all the fowls of the air, brought them to Adam to see what he would call them: for whatsoever Adam called any living creature the same is its name. 20. And Adam called all the beasts by their names, and all the fowls of the air, and all the cattle of the field: but for Adam there was not found a helper like himself. 21. Then the Lord God cast a deep sleep upon Adam: and when he was fast asleep, he took one of his ribs, and filled up flesh for it. 22. And the Lord God built the rib which he took from Adam into a woman: and brought her to Adam. 23. And Adam said: This now is bone of my bones, and flesh of my flesh: she shall be called woman, because she was taken out of man. 24. Wherefore a man shall leave father and mother, and shall cleave to his wife: and they shall be two in one flesh.'

Some points to notice in these verses are first that God noted it was not good for man to be alone and needed a 'help like himself', but no help was then made. First the animals were brought to Adam who named them, but none among them was suitable as a companion for Adam. It is clear that Adam's companion must

be near to him, suited to him and not a *mere animal*. At the time these passages were written woman in general was held in contempt, fit only to be a toiler for man, but verses 23 and 24 clearly reverse this view of the very low status of woman by showing how close Eve was to Adam—she was part of him; she had the same nature as he had. She was bone of his bone, flesh of his flesh, a suitable companion for him complementarily expressed in their union as man and wife which shall be so close that they shall be two in one flesh and a man shall leave father and mother to effect this union. Thus the essential truth here would seem to be that man and woman are equal in dignity and nature and made for each other.

Genesis teaches that Adam and Eve were very closely connected to each other, and the Biblical writer showed this in his own way by the metaphor of the creation of Eve from the body of Adam. But why this particular metaphor was used seems to be uncertain. In correspondence the Rev. L. Johnston¹ wrote:

If we remember that these chapters of Genesis are not the result of revelation to the author, but the inspired result of reflection on the existing state of humanity, we shall understand that he frequently presents an argument from effect as if it were an argument from causality—he elaborates his description of the origin of man, not on the basis of first-hand observation, but on the basis of the observed effects. The description of the creation of Eve, then, is intended to teach us her equality in nature with Adam and also a role secondary to him.

If such a metaphorical interpretation as we have given is valid, then a biological explanation may be sought which seeks the formation of Eve through biologically normal channels, and not through some unsound fanciful methods such as we have already mentioned. Some writers, such as M. Paquier,² considered that an early division of the embryo of Adam could have given rise to Eve much in the same way as identical twins are produced. Generally, however, identical twins are produced simultaneously in the very first stages of division of the fertilized egg. It is

¹ Father L. Johnston of Ushaw College has given me very great assistance in arriving at an interpretation of the relevant parts of Genesis and he has guided me all through this section on Adam and Eve, but the biological explanations are completely my own.

² See Abbé J. Gross, 1949, p. 144.

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scarcely possible to say that one has precedence in time over the other. Again, identical twins, by their very method of production, are always of the same sex. If one were male and the other female an explanation would have to be found for the differences in the sex chromosome mechanism, which is not easy to visualize. There may also be a philosophical difficulty in such an explanation which, of course, is present in any case regarding the origin of the human soul in identical twins. And while souls may not possess sex as we know it, in the production of Eve as visualized above, the original zygote must have possessed a substantial form of one kind and a short time later another different kind of form would have been present, unless one accepts the mediate animation theory, that is, the theory that the soul does not infuse the body until it is more or less recognizably human.

Another explanation of the formation of Eve may be given which avoids the biological difficulties involved in the methods mentioned so far. It may be possible that Eve was formed in the most natural way of all, that is, by the ordinary method of sexual reproduction. In the very first few generations of human beings 'marriages' must have been between very close relations. Such close unions could not in those days have been repulsive or un-aesthetic; indeed, they must have seemed natural and normal to the people involved. If, then, Adam was the product of pre-hominid parents acting as instrumental causes,¹ or of Pre-Adamites, if they existed, which may have been practically pre-hominids, and if he grew up among these prehominids very near to him in the physical sense, then he need not at first have been physically repulsed by the more advanced females among them, and thus he could have had a child. Later, perhaps even before this child was born, a psychic isolation mechanism may have arisen which prevented him from associating with other of these pre-hominid creatures.² The child produced in this way would then have been the product of a fully-formed human male gamete and a near-human female egg. As a single gamete itself contains *all* the potentialities of the offspring, the child would have been human in the true and full sense of the term, and could have received a human soul in the way we all do. It would have been formed *from* the body of Adam in the most natural and intimate way. Such a child could have been Eve. We may note also that such a

¹ See p. 319 and pp. 321-323.

² See also p. 193.

close union of Adam with Eve would, in the biological sense, enhance the specifically human qualities of their descendants by 'strengthening the breed' to use a genetical phrase. Inbreeding at this stage of humanity could only have been advantageous. Later, however, it would become partly disadvantageous if practised to any great extent.

Finally, Eve may have arisen in another natural way involving sexual reproduction. We have already mentioned that Adam could have arisen from the fusion of two very near-human gametes carrying the final mutations necessary for the completion of physical man and which were themselves produced from male and female near-human advanced prehominids. Such gametes would be potentially human. They would have arisen as the result of a single meiotic division in which segregation of the mutated chromosomes would have occurred in the normal way. In the normal way if a mother cell carries, shall we say, factors *Aa*, when meiosis is completed four nuclei are produced, two with *A* and two with *a*. Hence, in the hypothetical case we are considering, four gametes would have been formed in each parent, each carrying the necessary final mutations. Four of these would carry the *X* chromosomes from the female, and from the male parent two would carry one *X* chromosome and the other two the *Y* chromosome.

It is possible, and perhaps not unlikely, that when copulation occurred between these parents a double fertilization took place bringing together these potential human gametes carrying the *X* and *X* or *Y* chromosomes and acting as instrumental causes. Of course, two zygotes would result, one with *XX* chromosomes, or female, and one with *XY* chromosomes, or male. As fertilization is a random process, there is no reason why the *XY* combination should not have been produced first in time. The final result would be the birth of fraternal twins, one boy and one girl, and perhaps the boy would be born first, although strictly this would not be necessary. These children could then have been Adam and Eve and their subsequent marriage would perhaps not be so repugnant or difficult to picture. When we consider all the numerous factors in such a process as outlined above which would be needed to bring about such a concatenation of events, we see clearly that it is extremely unlikely, in fact practically impossible, for the process to be repeated exactly. The production

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of fraternal twins discussed above should not be confused with M. Paquier's idea of the formation of identical twins mentioned earlier. The processes involved are completely different and not strictly comparable.

Such biological explanations of the formation of Adam and Eve as we have given may seem to be as fanciful as those mentioned earlier, but in any case, they are not biologically unsound, or indeed unlikely, given the circumstances of the times. And they do account for the nearness of Eve to Adam and perhaps her dependence on him, and they are not contrary to evolutionary possibilities. No doubt such speculations tend to offend our aesthetic and perhaps psychologically preconceived ideas, but then, have we really any true reason for projecting our advanced ideas into the unknown mind of Adam?

2. EVOLUTION AND PHILOSOPHY: THE FAITH OF A CATHOLIC BIOLOGIST

Evolution and philosophy

Donald Nicholl¹ writing in the *Tablet* about a discussion on 'The Destiny of Man' in the *Sunday Times* already mentioned had this to say, and in spite of its length I give the whole paragraph.

During the past few centuries the ordinary Catholic has been rendered 'homeless' in the universe in the sense that the images in terms of which he lives his religious life have become unrelated to the concepts in which he is taught to think about events in space and time. Over the course of a thousand years saints, artists, thinkers and poets had built up for him a vision of the whole universe which gave him a focus, a hearth, a home wherein he could grow up, say his prayers, bury his dead and be buried, aware that he belonged, that he had a place. Nowadays, especially under the impact of the evolutionary images which meet him in films, television and radio, he has come to accept unconsciously the dictum of a famous biologist, that 'man is an excrescence on the face of the universe'. He is homeless, and if he is badly educated or not specially intelligent he feels completely unprotected outside the walls of the church. Is it not possible for Catholic biologists and palaeontologists to offer him a vision of the universe which will take in the discoveries of recent centuries

¹ 1918, p. 207.

and yet allow him to be at home amidst the images it offers? Or must our experts pass by on the other side of the road, leaving him homeless?

My own views and feelings merely echo those of Donald Nicholl expressed above and the compulsion I felt in producing this book was due to a desire to show that evolutionary biology is capable of leading a Catholic closer towards his Faith. That is why I have sub-headed this section *The Faith of a Catholic Biologist*, and I hope to justify this title in this last section and to go some little way in answer to Nicholl's appeal.

The writer here would like to emphasize again that, while he writes in this section in a philosophical vein, he is not a professional philosopher. In all philosophizing on scientific subjects there is always the danger of falling into error, but this is a risk we must all take. As W. M. Kyle¹ wrote: 'The greatest logical error which can be made by a scientist is to mistake the direction of the investigation upon which he is engaged and to impart into his descriptions or explanations hypotheses which, though perhaps relevant and adequate in another sphere of enquiry, may be quite wrongly applied to elucidation of the problem in hand.' But, throughout this book when any philosophizing has been attempted, it has clearly been concerned with the use of words, facts, hypothesis, or with an extended and derivative meaning which could legitimately be applied to the scientific topic under consideration. This is philosophizing, not on the scientific matter as such, but on the hidden concepts which the scientific facts or ideas call forth in our minds. In this way then I am merely philosophizing in the sense of 'thinking around' the subject, and I feel a compulsion to do so because I realize that the scientific theory of evolution deals with the history and origin of animate things only at the evidential and phenomenological levels. At these levels, I think, it is not intellectually satisfying; it seems to lack something; to be incomplete. As a philosopher may say, it does not touch on the 'essence' of things which is the realm of metaphysics. Many biologists know nothing of such essences—they find a sufficient explanation in the empiricism of their own scientific methods. This is a reasonable attitude to hold, providing one does not particularly wish to find a meaning in evolution,

¹ 1956, p. 159.

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or accepts a superficial meaning, which unfortunately, if developed, may lead to real difficulties. For example, trusting in evolution as giving an explanation of things, the evolutionist still finds it extremely difficult to show satisfactorily that spiritual man is not different in kind from the animal which his appreciation of the good, his knowledge of evil, his knowledge of truth and beauty, and most important, his striving after God, clearly indicate. In vain do some evolutionists strive hard to build up an evolutionary ethic,¹ but their attempts are not very convincing, and some people would say are even futile, because they seem to overlook the basic principle that the truth of moral principles cannot be derived from disciplines which are not moral. The primary validity of moral judgments cannot be derived from physical science.² We prefer to believe that evolution gives us a scientific account of the progress of living things and nothing more at that level, and this applies even more so to man whom evolutionists themselves acknowledge to be a unique creature. As soon as science leaves the observable and the measurable levels it is no longer science, but philosophy. Evolution and biology may tell us something about the nature of man, but in that aspect of himself which makes him unique, man must make use of that very uniqueness in order to attempt to fathom his nature. Man is not just an animal; he is a glorious creature made in the image of God. Unless then we can interpret evolution, unless we can get a meaning out of it, contributing in some way to an understanding of man's uniqueness, the theory will have little value for us beyond the realm of biology. Hence in this final section I attempt in a small way to interpret evolution as it appears to me.³

One of the most important features that becomes evident about any living creature is that it is an organism, it is an organic whole behaving in the way it does because of its organization. An organization may be said to be a state of relationship between parts which is theoretically discernible and subject to the laws of causation. It is a natural and realistic concept. Evolution is a study of beings in a state of becoming, and hence it connects to metaphysics. A modern writer,⁴ R. H. Phillips, came to the conclusion that purely materialistic evolution is impossible because it

¹ See J. Huxley, 1947; G. G. Simpson, 1950, and C. H. Waddington, 1942.

² See M. C. D'ArCY, 1944.

³ I have already begun this interpretation, see Fothergill, 1953, 1957.

⁴ 1934.

denies finality, and hence that other kinds of evolutionary theory must take account of teleology and purpose and of the action of the First Cause. On the other hand, a scientific theorist may find these concepts unnecessary in his work and may omit them. But both philosophy and the history of evolution show that the theorist would then be dealing only with a part of the evolutionary idea, and thus his conclusions could only represent a partial approximation to the truth. The theory of evolution at the phenomenological level neither affirms nor denies the philosophical, and particularly the metaphysical, connections. Again, Brisbois,¹ through a different approach, found that the problem of the origin of species is really a metaphysical problem of ontological causality. In the sense of one species changing into another, by which is meant that one species becomes a different *kind* of species, Brisbois in the light of scholastic teaching concluded that: 'In our opinion we can legitimately draw the conclusion that Transformism, understood in the sense explained, not only does not contradict the essential principles of the scholastic ontology, but indeed harmonizes very well with these.'

Ontological causality, however, is the proper study of metaphysics. Hence from this viewpoint also it would seem that biological evolution can never be complete of itself, and the deeper conclusions which biologists draw from a biological study of evolutionary processes can never be other than relative conclusions. They must evidently be reoriented with other relative conclusions from philosophy before the meaning of the concept can become known. A purely deterministic outlook on evolution would seem to ignore this relative aspect of the subject; a wider viewpoint is required. In this regard A. F. Taylor² remarked: 'Philosophy, no doubt, needs to make use of the concept of evolution, but a philosophy based on that conception must necessarily end in illusion.' A scientific study of evolution and its implications has already led at least one modern British writer on evolution, namely, Sir J. Huxley, to conclude that through evolution man has become at least partially 'spiritual', and by implication that there is a certain amount of 'spirituality' in evolution itself. A French-American writer, Lecomte du Nöuy³ seems to hold views of the same order. Both writers considered man to be at the head of the evolutionary process, and that evolution in the future will

¹ 1949, p. 122.

² 1932, p. 448.

³ 1947.

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take place through progress in his intellectual equipment and ideas.

If evolution is true, if the idea is sound, then evolution is good and the effect the process of evolution has on nature will be good. The evolutionary idea is outstanding in one thing, and that is, it gives us an impression of unity in animate nature. Through it the parts of animate nature are united in a cause-effect relationship and in this feature it agrees with other methods of the interpretation of nature. Thus, the effect of evolution is good. No other theory, or idea of the existence and relationship of living things, does this in the same degree. If sense data regarding the nature of living things tend to the conclusion that living things are organisms of particular kinds, then the sense data of evolution tend to show that changing living things are *patterned organisms* moving in a definite direction. The individual living thing exists as an actual being, but because of its relationship to its ancestors and to its descendants, the organizational pattern of the living actuality also possesses potentiality. It is always in a state of becoming, a state of becoming actual through growth and a state of becoming different through development and evolution. A patterned organism shows motion in a high degree.

The consideration of evolution as a sequence of changes among living things indicates very plainly that evolution itself has a pattern, and the lines of this pattern move inexorably in one direction towards an increase of complexity in individual patterns. So that patterned organisms are produced which represent the acme of development of particular patterns in particular surroundings. The organism has to be adapted to live. The greater ease with which a particular organism overcomes a variety of changing surroundings, then the greater the complexity of that organism and hence of its pattern. This last idea, perhaps, represents the real meaning of perfection in animate things. But only one patterned creature is able to rise above his surroundings so much as to seek to control them. And, of course, that creature is man. Man as an animal shows himself to be the most complex of beings, and thus he represents the highest stage in the evolution of patterned organisms. He would never have got beyond this stage of physical man, and may even have died out, if he had not come to possess this ability to rise above and to control his surroundings. This feature which makes man pre-eminently perfect and adaptive

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is his rationality or, to express it in a more specific way, his *intellectual spiritual soul*. Hence the true interpretation of evolution becomes bound up with the nature and purpose of man.

If we remember (a) that man as an animal is just a complex one depending for his animality on his patterned organismal condition, and (b) that in the evolutionary line his pattern has developed to produce an animal which is potentially capable of rising out of the sequence of ordinary biological events, then we can see plainly that the advent of the intellectual soul was a unique event in the natural world. It was an event which was not potentially present in cosmic nature *qua* nature, an event which was transcendent to the normal process.

The Christian religion and philosophy necessarily maintain that each human intellectual soul is truly a unique creation in the absolute sense. If this were not true the whole basis of that religion would be undermined. The soul is immaterial and not susceptible to direct investigation by empirical methods. Science is neutral regarding it, but need not ignore it. Hence we may say that the creation of a new spirit, which, when infused into a certain one of the end-products of evolution, that is physical man, formed an intellectual soul and produced the first rational human being. The human soul thus has no necessary connection with the life principle, or organization, of the organisms that preceded its creation (except in so far as this organization was perfect enough to receive the soul). Hence there was no break in the chain of nature as such, for the advent of the human soul is a fact above ordinary natural happenings; it is a gratuitous addition to nature. This is a reasonable conclusion for a theist, but it seems to be one which pantheists are unable to arrive at because of their identification of nature with God. On our interpretation man is a spiritual and physical creature, but his spirituality is such as to allow him to develop, or evolve, along a plane which by definition has no necessary connection with the purely physical sequence as we experience it.

Evolution is invariably conceived both by biologist and philosopher as a continuous process. And this is probably true. It is said then that the advent of the human soul would introduce discontinuity, would break the chain of nature. In other words that it would constitute an interference with the course of nature. While in no way denying the possibility that God may 'interfere'

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with His own creation if He so desires,¹ I suggest that the creation of the first human soul, that of Adam, was not a break in the evolutionary line (see later).

St. Thomas² wrote:

Now, in the actualizations of forms, there is a certain gradation. For prime matter is first in potency to the form of an element, and when it exists under the form of an element, it is in potency to the form of a compound; considered under the form of a compound it is in potency to a vegetative life principle, for the (vegetative) soul is the actuality of such a body. Again, the vegetative soul is in potency to a sensitive, and the sensitive soul to an intellectual soul, as is shown by the process of generation. For in the first place, in generation the fetus lives with the life of a plant, afterwards with animal life, and finally with human life. But beyond this form there is no further or more worthy form in things capable of generation and corruption. Hence the ultimate stage of the whole process of generation is the human soul, and to this matter tends as to its ultimate form. Thus elements are for the sake of compound bodies, and these in turn for living beings, in which plants are for the sake of animals and animals for man, man being the end of the whole generation.

Thus St. Thomas argued that man is the end-point of the earthly scheme of things. In the line of perfection there is a scheme ending in the most perfect earthly being which is man, and all things are for his good and use. In the biological field some biologists, including Sir Julian Huxley, have argued that major evolution of plants and animals has ceased. Man is also the end-point of the evolutionary scheme, and he is the dominant creature on earth. With his mental powers he would see to it that no other creature evolved sufficiently to gain dominance over him. On the biological level we see that the various groups of animals have become specialized along certain lines which they pursue until they become over-specialized. Evolution shows that they are then naturally selected against and die out.

Man, on the other hand, is not particularly specialized in the physical sense. Evolutionists invariably hold that his body is rather generalized than specialized and indeed contains many primitive features. Thus his body remains plastic. His specialization lies in his brain, and the very specialization of this

¹ Even in miracles God does not, strictly speaking, 'interfere'. 'Miracle' is only a word ordinarily used to describe the highly unusual. God maintains all nature in being and in action and He cannot therefore interfere.

² *Summa contra Gentiles*.

structure has given him the realization of his power. The conclusion from these considerations is that man's further evolution lies only in the evolution of his mental powers towards his psycho-social betterment, and towards the control of the evolutionary process itself. Before the Fall Adam may have been intellectually and spiritually superior to us, and it is reasonable then to consider that major evolution ceased with him. We may say the chain of major evolution reached its natural end with the advent of Adam. From amoeba to physical man, as it were, the chain was complete and continuous. God may have willed the process to cease there, but instead something new was created, something which was not part of the purely biological process occurred; in the true sense of the word God created an intellectual spiritual soul to inform the physical end-point of the animal body. It must not be thought that this process of the infusion of the human soul necessarily implies that man is dualistic, made up of two beings—a soul which happens to inhabit a body, as it were. This is not so, but may appear so because of the difficulty of finding ordinary words to express it. A man is just one being. The explanation can be given by Thomistic philosophy which identifies the soul with substantial form and the form is that which makes a thing what it is. The human soul is essentially different in kind to other forms. This point was well expressed by L. Bright to whom the reader is referred for a short review. Bright¹ wrote: 'Soul is simply that which by informing matter makes a being such as we are, who, like the other animals, grows, feels, sees, thinks, thanks to a structure biologically describable. But there is a human activity that differs from that of the animals, the activity of knowing and willing, and this requires us to say that the human form, while it is still all that animal form was, has also become something radically different.' We must also remember that at death the human soul becomes separated from the body and exists as a distinct entity. The creation of this radically different entity is not then a break in the natural continuity of an evolutionary process which had reached its natural end on the level of the animal. A similar creation occurs whenever a baby is produced. It is in fact an addition to the evolutionary process and not an interruption of it, as we have already mentioned.

Thus, we may say, in the evolutionary picture we have drawn,

¹ 1939, p. 124.

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the unity and uniformity have not been upset. The laws of nature have not been upset. These laws remained as they were, dynamic up to the point which was their natural end, but henceforth static, until something not subject to them was imposed on the life continuum. And so the patterned organism became a spiritual and hence *free being* with a power of moral activity and with an immense potentiality for development (or evolution) of that unique feature which made him free. Evolution may thus be said to have a certain 'spirituality' about it, because it helped to produce this free being. Intellectual and spiritual freedom is a gift which expresses itself only through the brain or mind, because it may be thwarted in diseased brains, but it is not just a mental concept, or process. It is something fundamentally independent of mere mentality because it may, and often does, find its highest expression in people of less than average mentality. It seems that there is a pattern in freedom too, and hence it may develop differently in different individuals.

Although freedom in an individual may be absolute in the sense that he may make a choice, it is also relative in that he must choose between things or ideas proposed to him. It is the pattern of freedom which seems to be concerned with this relative aspect, and, if freedom represents in a word the differentiation of man from the rest of the animate creation, then the pattern of freedom can only work towards a perfection of itself, which will be seen as an enhancement of his moral and spiritual activities. Being free it can only become more free at a higher level. And, except for the more mundane and humanitarian aspect of ensuring that all men are allowed the right use of freedom in the relative sense, this seems to be as far as mere evolutionary ideas can take us.

In conclusion we may say that the materialist evolutionist accepts views of evolution leading to the conclusion that man is the supreme product of the process, and that by further evolution he should endeavour to direct the process through his experience, knowledge and ability to transmit these to future generations, to produce a better race of men which may attain to more happiness and good living than we enjoy. Possible lines of approach to, and attack on, the problem of the control of human evolution have indeed been seriously outlined by C. D. Darlington.¹ In the previous section we mentioned a series of articles in the *Sunday*

¹ 1938, pp. 14-17.

*Times*¹ begun by Sir Julian Huxley. We welcomed the recognition that man is a unique creature possessing what Huxley called 'spirituality'. In the last article of this series, however, Sir Julian considered religion last. Having given complete pre-eminence to evolution he could see religion only in the light of evolution and so he fell into pantheism. According to Sir Julian, the old religions are due to be swept away, and a new religion must be evolved. He said: 'So far as I can see, the only chance of securing a religion which will unite humanity instead of dividing it is to build it round the concept of evolutionary fulfilment, with belief in human possibilities as its central core and scientific method as its chief weapon.' To a man of religious Faith this is a ghastly picture ignoring the highest human aspirations, and it shows clearly that the meaning of the Christian religion has not been attained. The 'spirituality' which is found in evolution is obviously not the same as true spirituality according to its old meaning, and yet the mere use of the word in an evolutionary context is an indication that there is something beyond evolution which is to be sought after. If I may express it this way, the error in Sir Julian's interpretation of evolution lies in 'deifying' it by considering that evolution is the *ultimate* force of the universe. This perhaps is due to an underestimation of the true nature of spiritual man and of the spiritual and biological meaning of the Incarnation.

Between evolutionary materialists or agnostics of this kind and the Catholic or Christian biologist lie the tremendous facts of the Incarnation and the Redemption which alone are the Hope of mankind. History shows only too plainly that without these man himself merely destroys his kind. The Catholic, however, can readily subscribe to the furtherance of human happiness, providing it is happiness, and to the betterment of living conditions, because these things are good in themselves. But, at the beginning and end of all his activities he places God, his Creator, Who made him to know Him, love Him and serve Him for ever. Near the beginning of this chapter we began by pointing out that the Incarnation and the Redemption were the central pivots of Christianity. We were redeemed by Jesus Christ who is God and man. The Second Person of the Trinity took to Himself a human nature in order to undo the sin of Adam. It is this vitally im-

¹ 1958.

EVOLUTION AND CHRISTIANS, CONTINUED

portant fact which changes everything, without which human life is empty and meaningless, but which, when acknowledged in Faith, gives direction, fullness, hope and purpose to our lives. Christ is perfection itself, and may we not imagine that the human body ready to be infused by the human soul had itself also reached such a state of physical perfection as to fit it to be the future abode of Christ. The fact that Christ became man is itself an indication that man in his body is the end-point of evolution.

Thus the conception of an evolutionary process in nature which is a product of the Divine Will posits the answers to the enigmas of life and its progress. Life as we know it by experience is a material phenomenon, and in conjunction with evolution, we may say that it has led to the production of a material being, or end-point, in the process which is capable of being united to the immaterial but yet distinct. J. L. Russell¹ wrote:

We can prove with complete certainty the existence of an Omnipotent, Eternal, Necessary Being from the existence of matter and motion, both of which, like everything else, were created by Him, are conserved by Him, and are subject to His will in all things. Once this is clearly recognized, the question whether or not the whole realm of physical nature was produced by purely natural laws becomes, from the theological point of view, unimportant. What is certain and important is that God intended, from all eternity, to create Man and to put him in this world as the crown of this particular order of creation, and that He took those means which He saw to be most suitable for the purpose. As time goes on, we may hope to see ever more clearly what those means were. We have no cause to be alarmed at the prospect that they may have been the ordinary laws of nature.

Life leads to Man, and man has become endowed with a spiritual nature which sets him apart from his material antecedents, but does not obliterate them.²

¹ 1916, pp. 44-45.

² Since the above was written an English translation of Teilhard de Chardin's *Le Phenomene de l'Homme* has been published (1939). In this outstanding and penetrating study of man which seeks for the first time to give an over-all intellectual explanation of the meaning of evolution in terms of man and the cosmos, it is interesting to note that Teilhard finally attempts to relate evolution to the transcendent fact of the Incarnation. As he says (p. 297): 'Christ invests himself organically with the very majesty of his creation. And it is in no way metaphysical to say that man finds himself capable of experiencing and discovering his God in the whole length, breadth and depth of the world in movement. To be able to say literally to God that one loves him, not only with all one's body, all one's heart and all one's soul, but with every fibre of the unifying universe—that is a prayer that can only be made in space-time.'

'O God, Who in creating human nature didst wonderfully dignify it and still more wonderfully reform it, grant that by the mystery of this water and wine we may be made partakers of His Divinity Who deigned to become partaker of our humanity . . .' In Christ we contemplate the mystery of the union of two Natures, the Divine Nature and the human nature. In the Mass we symbolize this mystery by mixing wine and water with the above prayer which also asks for us to become partakers of the Divine Nature. God created human nature and still more wonderfully reformed it. By analogy might not the union of the highest patterned organism with the unique intellectual and spiritual soul of preternatural man symbolize also the Incarnation and give us a reason for our animal and spiritual nature? We are made in the image and likeness of God, and our ultimate purpose is a spiritual one which transcends our animal one as Christ's Divinity transcends His humanity. In terms of evolution materiality has ceased and immateriality has taken over. We may advance further in the realm of the intellect wherein we become truly free. Thus, knowing we have life within us, and knowing we are evolved creatures specially chosen to make a free choice, the highly evolved man turns to the source of his power. Biology and evolution, then, wedded to a philosophy of universal concepts, give an interpretation of the highest potency, leading to lofty aspirations which lie only in the cultivation of the intellect towards the Absolute Good.¹ A consideration of life and its progress naturally leads us to the nature and purpose of man which is to love God. Our further development thus lies along lines which develop and concentrate our love of God; in a word along the line of sanctity in all its many aspects and by doing so we may achieve our spiritual and evolutionary destiny. Anything else is either contrary to this God-willed scheme of evolution, or is neutral and ineffective.

¹ Since writing the above I have read E. L. Mascall's *Christian Theology and Natural Science* (1956) in which very similar views and sentiments to those given in this chapter are much more ably expounded.

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FULL reference to books and papers mentioned in the text will be found in this bibliography. To find any particular reference refer to the date in the footnote at the bottom of the appropriate page in the text, or given in brackets after a name in the text, then look in the bibliography under the name concerned with the year corresponding to the footnote. As far as possible only standard abbreviations are used for all periodicals. These abbreviations will be found in the *World List of Scientific Periodicals*, 3rd. ed., by W. A. Smith, F. L. Kent and G. B. Stratton, publ. Butterworth Scientific Publications, London, 1932.

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